COMPARATIVE ECOLOGY OF BOBCAT, BLACK BEAR, AND FLORIDA PANTHER IN SOUTH FLORIDA

By

DAVID STEFFEN MAEHR

A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

1996

ACKNOWLEDGMENTS

This document was as much a family effort as it was a personal one. Diane Maehr, Clif Maehr, and Erin Maehr all shared with me the tribulations and triumphs of my most recent scholarly adventure. Without them, the task at hand would have been meaningless, so to them this dissertation is dedicated. As no less a part of our family, Herbert W. Kale, II was always a close friend, trusted advisor, and supporter of my return to school. His untimely death in 1995 left many questioning their purpose in life; now his memory is a guiding beacon.

Many people have contributed to our current understanding of carnivore ecology in south Florida. Those who were particularly helpful to me in this endeavor include E.D. Land, Todd Logan, J.C. Roof, J.W. McCown, and J.N. Layne. R.T. McBride, and frequently his sons Rocky and Rowdy, linked us with study animals and maintained the research momentum. I am also grateful for the opportunity to have worked with M.E. Roelke, C.M. Glass, M.Lamm, T. Ruth, S. Citino, and especially J. Lanier, all of whom helped to look after anesthetized bobcats and panthers. J. Kappes, R. Bell, and P. Baronoff were important field assistants who lent their unique personalities to the project. S.C. Maehr and E.N. Maehr were special assistants during captures of black bears, as were L. Richardson and K. Edwards. O.L. Bass provided insightful views on wildlife from southeast Florida, and I appreciate many conversations over the years with M. Hornocker and D. Wesley on the subjects of panther biology and politics.

I thank the Florida Game and Fresh Water Fish Commission for allowing me to be a part of its celebrated research efforts and for providing the funding instrument on behalf

of the people of the State of Florida, and the citizens of the United States. I appreciate the interactions I had with all of this ageny's staff, but R.M. Brantly, A.L. Egbert, F. Montalbano, III, and T.E. O'Meara were particularly helpful. The U.S. Fish and Wildlife Service, Florida Department of Environmental Protection, National Park Service, and the Seminole Indian Tribe facilitated access to their vast holdings of publicly owned land. Of equal, if not greater, importance was the access to private properties and the assistance of their managers and owners including W.B. Lester, B.H. Griffin, E. Carlson, E. English, L. Gable, B. Collier, M. Scofield, J. Fitzpatrick, T. Baker, J. McDaniel, D. Pylant, M. Ramsey, J. Hendrie, E. and J. Smoak, J. Hilliard, and J. Billie.

Committee members W. Kitchens, F. Mazzotti, J. Mullahey, and E. Jacobson provided much-needed encouragement throughout my doctoral program. In particular, M. Sunquist, and J. Eisenberg challenged me with provocative thoughts and helped draw new ideas out of me. I am especially indebted to L.D. Harris who was one of my first acquaintances in Florida and who has never let me relax for long. His visions of the way things were and the way they should be have benefited many ecological disciplines and everyone he has worked with. His abilities to compel, cajole, and convince are equally matched by his willingness to listen, learn, and change.

Others who have helped me along this path in meaningful ways include K. Deagan, J.A. Cox, G. Tanner, F. Percival, P. Hall, M. Moulton, C. Arnold, E. Hellgren, C. Abercrombie, P. Walsh, and J. "Loquacious" Schortemeyer. My fellow graduate students G. Caddick, G. White, and especially T. Hoctor, provided free-flowing constructive criticism and comic relief at strategic moments.

I am particularly grateful to my employer and coworkers D.S. Wilkison and A.G. Simpson who have the extraordinary ability to see beyond the proverbial bottom line. P. Kennedy, S. Guajardo, R. Dichio, J. Davidson, R. McCormick, J. Wilkison, Joan Wilkison, and H. Wilkison were also very supportive of my return to school and helped me survive it.

Finally, I thank my parents, Carol and Robert Maehr, for sharing the excitement of my education, and my siblings, Brandt, Ted, and Jenny, for thinking no less of me for my efforts.

TABLE OF CONTENTS

	page
ACKNOWLEDGMENTS	ii
ABSTRACT	vii
Chapter 1. INTRODUCTION TO THE SPECIES AND THE STUDY AREA	1
Study Area	14
Summary of Previous Large Carnivore Work in Florida	22
General Methodology	30
Chapter 2. DIETARY OVERLAP	32
Methods	32
Results and Discussion	34
Species Comparisons	49
Chapter 3. HABITAT USE	54
Methods	56
Results and Discussion	60
Chapter 4. HABITAT PATTERN AROUND FLORIDA PANTHER NATAL DENS AND BLACK BEAR WINTER DENS	87
Study Area and Methods	88
Results and Discussion	89
Influence of Roads	104
Chapter 5. HOME RANGE AND LAND TENURE	109
Methods	111
Results and Discussion	113
Annual Comparisons	116
Seasonal Effects	116
Home Range Fidelity and Replacement	163
Overlap Within and Among Species	185
Chapter 6. DISPERSAL CHARACTERISTICS	204
Methods	205
Results and Discussion	208
Adults and Dispersers Compared	216
Chapter 7. SYNTHESIS AND CONCLUSIONS	263
The Return of Native Canids to Florida	270
A Longer Range View	278

Table of Contents (continued)

page

Appendix A. STATUS OF COYOTES IN SOUTH FLORIDA..... 293

Appendix B. MASS GROWTH IN BLACK BEARS FROM SOUTHERN LATITUDES..... 303

Appendix C. FLORIDA PANTHER POPULATION GROWTH..... 315

Appendix D. THE FLORIDA PANTHER: ALL PRESENT AND ACCOUNTED FOR?..... 331

Appendix E. VITAL STATISTICS OF SOUTH FLORIDA PANTHERS 1981--1993..... 338

Appendix F. VITAL STATISTICS OF SOUTH FLORIDA BLACK BEARS 1986--1993..... 341

LITERATURE CITED..... 343

BIOGRAPHICAL SKETCH..... 373

Abstract of Dissertation Presented to the Graduate School of the University of Florida in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy

THE COMPARATIVE ECOLOGY OF BOBCAT, BLACK BEAR, AND FLORIDA PANTHER IN SOUTH FLORIDA

By

David Steffen Maehr

August 1996

Chairman: Lawrence Dean Harris
Major Department: Wildlife Ecology and Conservation

Comparisons of food habits, habitat use, and movements revealed a low probability for competitive interactions among bobcat (Lynx rufus), Florida panther (Felis concolor coryi), and black bear (Ursus americanus) in south Florida. All three species preferred upland forests but consumed different foods and utilized the landscape in ways that resulted in ecological separation. Further, panthers exhibited crepuscular activity whereas black bears were predominantly diurnal. Seasonal variation in diet, movements, and reproduction were extensive for all species. In addition, high primary productivity, year-round food availability, and a warm climate encourage mass growth rates in south Florida black bears that exceed those of other North American black bear populations.

Subadults of all three species demonstrated extensive dispersal abilities, but only male black bears were documented to have crossed the Caloosahatchee River, a potential landscape barrier that may restrict effective dispersal northward in bobcats and panthers.

Because bobcat and black bear in south Florida occur at relatively high densities, anthropogenic changes to the landscape and sea level rise will affect them less severely

than panther. The problems associated with the habitation of a naturally fragmented and patchy forest are exacerbated by the conversion of productive habitat types to types that are avoided. Another factor that threatens the stability of ecological relations among this carnivore community is the range expansion of the coyote (Canis latrans) into south Florida. This canid is known to exhibit interference competition with bobcats, black bears, and panthers in other parts of North America. The diet of coyote in Florida may overlap with the diets of the three native carnivores by at least 38% and as much as 64%.

The highest concentrations of black bears and panthers in south Florida coincide with an extensive forest, a landscape feature that accounts for only a small proportion of public land. Increasing forest fragmentation from the Sarasota area southeastward suggests that most public lands are relatively unimportant to the two larger species. Because the demographics of even the smallest of these populations (panther) are shown to be typical of healthy populations, creative management such as flexible reserve boundaries and the enlistment of private property owners in conservation efforts may be of more immediate value than symptom-oriented management practices such as genetic introgression.

CHAPTER 1

INTRODUCTION

The terrestrial mammalian carnivore communities of pre-European temperate North America consisted of 35 species belonging to five families (Table 1.1). The prehistoric distribution, abundance, and associations of these species were a function of the interaction of climate, plant succession, competitors, and prey demographics (Harris 1988); factors that are all directly linked to geography and productivity of the landscape (Harris 1984:11-23, Zonneveld 1990). Although primitive humans (Homo sapiens) were a significant competitor with, and predator on, many of these species, post-Columbian humans have been much more effective than their predecessors in reducing native carnivore abundance and diversity throughout the continent (Diamond 1992). Recent local extinctions of large carnivores and a relative overabundance of meso-mammals throughout the southeastern United States have resulted from anthropogenic influences that include species introductions, overharvest, and habitat fragmentation.

There were 11 mammalian carnivores native to post-Pleistocene Florida (Table 1.1). The red wolf (scientific names appear in Table 1.1) has been extirpated due to overharvest and habitat alterations (Nowak 1991, Robson 1992) and the Caribbean monk seal is extinct, primarily because of overharvest (Wing 1992). The remaining species represent a nearly intact assemblage that has persisted to the present, despite Florida's

Table 1.1. The terrestrial mammalian carnivora of North America north of Mexico presumed to be present at the time of European colonization. Mass estimates represent species means (female and male), and were derived from Walker (1975), Burt (1975), and Chapman and Feldhammer (1982).

Species	Mass	Status in Florida
URSIDAE		
Black bear (Ursus americanus)	150 kg	threatened
Brown bear (Ursus arctos)	250 kg	not native
Polar bear (Thalarctos maritimus)	300 kg	not native
CANIDAE		
Gray wolf (Canis lupus)	42 kg	not native
Red wolf (Canis rufus)	25 kg	extirpated
Coyote (Canis latrans)	15 kg	naturalized/introduced
Red fox (Vulpes vulpes)	5 kg	naturalized
Kit fox (Vulpes macrotis)	2 kg	not native
Gray fox (Urocyon cinereoargenteus)	4 kg	resident
Arctic fox (Alopex lagopus)	5 kg	not native
PROCYONIDAE		
Cacomistle (Bassariscus astutus)	1 kg	not native
Raccoon (Procyon lotor)	10 kg	resident
Coatimundi (Nasua nasua)	9 kg	not native
MUSTELIDAE		
Ermine (Mustela erminea)	100 g	not native
Least weasel (Mustela nivalis)	50 g	not native
Long-tailed weasel (Mustela frenata)	200 g	resident
American mink (Mustela vison)	1.1 kg	resident
Black-footed ferret (Mustela nigripes)	1 kg	not resident
American pine marten (Martes americana)	750 g	not resident
Fisher (Martes pennanti)	3.5 kg	not resident
Wolverine (Gulo gulo)	20 kg	not resident
American badger (Taxidea taxus)	8 kg	not resident
Spotted skunk (Spilogale putorius)	700 g	resident
Western spotted skunk (Spilogale gracilis)	700 g	resident
Striped skunk (Mephitis mephitis)	2.5 kg	resident
Hooded skunk (Mephitis macroura)	2 kg	not resident
Hog-nosed skunk (Conepatus mesoleucus)	3 kg	not resident
Hog-nosed skunk (Conepatus leuconotus)	3 kg	not resident
River otter (Lutra canadensis)	8 kg	resident
FELIDAE		
Lynx (Lynx lynx)	10 kg	not native
Bobcat (Lynx rufus)	10 kg	resident
Ocelot (Felis pardalis)	13 kg	not resident
Margay (Felis weidii)	2.5 kg	not resident

Table 1.1. (continued)

Species	Mass	Status in Florida
Jaguarundi (Felis yagouaroundi)	7.5 kg	not resident
Puma (Felis concolor)	60 kg	resident
Jaguar (Panthera onca)	80 kg	not resident

quickly growing human population. It is a testimony to the difficulties of settling a wet, hot, and flat landscape that three out of five large (≥10 kg) terrestrial carnivores persist in south Florida. It has been only 70 years since highways were built to bisect this previously impenetrable wilderness (Carter 1974), and there is nowhere else in eastern North America where bobcats (Lynx rufus), black bears (Ursus americanus), and Florida panthers (Felis concolor coryi) continue to co-inhabit a single area.

Although the three large carnivores native to south Florida have been studied previously, none of the ecological studies exceeds more than a few years. Further, no analyses have examined them as an interacting community that inhabits the same landscape. Therefore, the objectives of this study were as follows:

1) Describe the spatial dynamics and habitat requirements of resident adult panthers, black bears, and bobcats in a rapidly developing south Florida landscape.
2) Analyze, compare, and contrast the use of space of resident carnivores with that of dispersing subadults.
3) Discuss the long-term prospects for the large carnivore community in south Florida with respect to landscape and biotic changes that are under way.

Overview of Carnivore Community Studies

Because of the difficulty in capturing and studying large carnivores, investigations of multi-species predator communities are sparse relative to studies of individual species.

Mutualism between predators and non-prey/non-competitor species has been documented only as anecdotes for bobcats and gopher tortoises (Gopherus polyphemus)(Winegarner 1985b), black bears and tufted titmouses (Parus bicolor) (Smith 1985a), and black bears and cattle egrets (Bubulcus ibis) (Smith 1985a). While these observations suggest unexpected relations between species, they likely occur too infrequently and at a scale too small to be important in affecting landscape conservation planning.

Few detailed studies of multiple-species carnivore assemblages have occurred in settings conducive to direct observation. Schaller's (1972) study of the African lion (Panthera leo) included detailed accounts of interactions among five Serengeti predators. Competition appeared to be reduced in that community by differences in habitat use, temporal separation, prey preferences, prey size, and hunting methods. Kruuk and Turner (1967), Bertram (1979), and Hanby and Bygott (1979) observed similar patterns among lion, leopard (Panthera pardus), cheetah (Acinonyx jubatus), and wild dog (Lycaon pictus) in the Serengeti.

Mills (1984) found that the four large predators in the Kalahari coexisted by reducing competition. Although lion and spotted hyena were mostly nocturnal and fed on similar species, they targeted different sex and age classes. Cheetah and leopard, on the other hand, exhibited temporal habitat separation and the leopard had a more varied diet than its likely competitors. On the other hand, in the Kalahari Gemsbok National Park, extremely high dietary overlap among lion, leopard, cheetah and spotted hyena (Crocuta crocuta) was caused by relatively low prey species diversity (Eloff 1973). Mills and Mills (1982) found that brown hyena (Hyaena brunnea) and spotted hyena became direct

competitors only when both were forced to rely on scavenging. Inverse relations in abundance have been observed or inferred between pairs of Old World predators. Myers (1977) found that cheetah were more abundant where spotted hyena were absent or scarce. When both species competed for Thompson's gazelle (Gazella thomsoni), their preferred prey, the cheetah was at a disadvantage and usually declined in number.

Seidensticker (1976) found that tiger (Panthera tigris) and leopard in Nepal exhibited nearly total ecological separation from each other by consuming different-sized prey, by using different habitat, and by exhibiting different patterns of activity. Only where prey were abundant did these two species coexist in similar habitats. A study of leopard and caracal (Felis caracal) in South Africa showed that these species avoided competition by utilizing mutually exclusive habitat types (Norton and Lawson 1985).

In South America, direct observations of interactions between species are nearly impossible due to the dense vegetation that many forest carnivores inhabit. At the same time, the very environmental conditions that hamper the development of ethograms, have likely affected the way these species utilize their landscape. Interestingly, while most studies of carnivore communities in the Old World tropics inferred several levels of competition among sympatric vertebrate predators, the opposite appears to be the case in the New World tropics.

Konecny (1989) examined a small carnivore community in Belize that lacked obvious competitive interactions. Jaguarundi (Herpailurus yagouaroundi), tayra (Eira barbara), ocelot (Felis pardalis), and margay (Felis wiedii) coexisted without using similar habitats and with little dietary overlap. Puma, jaguar (Panthera onca), and ocelot avoided

competition by means of prey size partitioning and habitat specialization (Schaller and Crawshaw 1980, Rabinowitz and Nottingham 1986, Emmons 1987). Sunquist et al. (1989) found that ocelot, hog-nosed skunk (Conepatus semistriatus), tayra (Eira barbara), grison (Galictis vittata), and crab-eating fox (Cerdocyon thous) avoided competition in Venezuelan llanos through diet partitioning.

The importance of the grizzly bear (Ursus arctos) in the sclerophyll community of the western North America was considered sufficient to include its common name as part of Shelford's (1963) ecological classification of North America. Its predominance resulted in the virtual exclusion of the black bear. But through time and coincident with the decline of its larger competitor, the black bear is now widespread in this part of the grizzly bear's former range. Herrero (1978) suggests that evolutionary processes resulted in differences in form and behavior between black bear and brown bear. Larger size, more aggressive behavior, adaptations for digging, and the inability to climb trees suit the brown bear to life in more open habitats than the forest-dwelling, tree-climbing, more demure black bear. The separation of these species was maintained by historic patterns of forest cover and the brown bear's dominance over the black bear. In most cases where overt interactions have been reported, the brown bear was dominant (Mattson et al. 1992, Ross et al. 1988).

Giant panda (Ailuropoda melanoleuca) and Asiatic black bear (Ursus thibetanus) exhibit a high degree of spatial overlap and similarity in size and form, yet exhibit divergent food habits and feeding strategies (Schaller et al. 1989). Despite having similar digestive systems, the giant panda is a food specialists, while the Asiatic black bear is a

food generalist. No competitive interactions between these species have been reported. Johnson et al. (1988) reported that red panda (Ailurus fulgens) and giant panda overlapped in space but have evolved very different energetic and behavioral strategies that allow them to utilize different plant parts.

Sympatric carnivores throughout the world exhibit a multitude of strategies for themselves in environments of limited resources. When a common resource is utilized by more than one species, co-occurrence is facilitated by differences in habitat use, and/or activity pattern. These patterns change with size of prey, size of predator, number of potential competitors (Rosenzweig 1966), climate, group size, and human influences. Schoener (1974) generalized that resource partitioning was most often accomplished by means of separation along habitat dimensions rather than temporal dimensions. However, his review focused primarily on invertebrates, birds, and small mammals, and did not consider the diversity of species aggregations characteristic of mammalian carnivores. Case and Gilpin (1974:3076) suggest that the relative costs of exploitation- versus interference-competition favored the latter in part because "the contraction from the fundamental niche to the realized niche is likely to be small for an interference competitor and high for an exploitation competitor." This pattern appears evident in the Old World tropics where dominance hierarchies among predators have been frequently observed, but is less apparent in the New World tropics. More diverse landscape features, most specifically topography and vegetation, have offered very different milieus for community evolution and likely have exerted a powerful force on the nature of resource partitioning among sympatric carnivores. At the risk of oversimplification, communities evolving in

landscapes dominated by unforested expanses (e.g. East Africa) tend to exhibit more interference competition than species complexes co-evolving in dense expanses of forest cover (e.g. South America, Southeast Asia). The aggressive and dominating nature of the brown bear in lightly-forested terrain is an example of this process in North America. For other North American carnivore communities, human-caused changes to the landscape have affected the patterns of community organization and resource partitioning through recent losses and additions to local carnivore faunas.

South Florida offers a variety of land cover types including expansive areas of open, herbaceous vegetation and extensive systems of dense forest. The three remaining species of large terrestrial carnivores that are native to this area all confine most of their activities to plant communities contained within or immediately adjacent to forest cover (Maehr et al. 1991a, Foster 1992, and see habitat use chapter). The recently extinct red wolf may have made more use of relatively open terrain, a trait that may have facilitated its extirpation. In recent years the coyote has become a more noticeable component of the current carnivore assemblage (see Appendix A), but little is known about its diet, distribution, and habitat needs in South Florida.

Studies of large carnivores consistently support the notion that the conservation of these species is a landscape-level issue. Although proposed solutions to the problem of shrinking wildlife habitat have stimulated debate (Harris and Gallagher 1989, Simberloff et al. 1992), all potential approaches are land extensive. Spatial requirements of Florida panthers and black bears are enormous. Annual home ranges of individual adult male panthers can exceed 500 km^2 (Maehr et al 1991a) and one-way dispersal movements of

black bears can exceed 140 km (Maehr et al. 1988). Telemetry studies of south Florida carnivores span 15 years, yet government agencies are just now attempting to apply these findings to management (e.g. Cox et al. 1994). Progress in landscape-level species management is limited but includes construction of wildlife underpasses and the purchase of the Florida Panther National Wildlife Refuge in Collier County.

Unfortunately, the treatment of symptoms will fail to correct the root problem facing terrestrial carnivores in Florida: that being the large scale alteration of the landscape. Inexorable human development of private lands in south Florida has the potential to eliminate 45% of presently occupied panther range and reduce the existing population by well over 50% (Maehr 1990). Although the black bears of Collier County appear to be tolerant of many anthropogenic changes to the landscape, most people will not tolerate their presence. The result is a high rate of mortality and injury to bears inhabiting the urban/wilderness interface. Bobcats are commonly reported as predators of domestic livestock throughout Collier County and can still be legally eliminated consequent to these depredations.

All three of these species have been studied extensively throughout their ranges (Anderson 1983, Anderson 1987, Pelton 1982) in North America. In Florida, published bobcat investigations, mostly in the vicinity of the Lake Wales Ridge, span two decades (Table 1.2). However, concern over the impact of the fur trade on bobcats (National Wildlife Federation 1977) led to extensive field work to detail population status and trends (Florida Game and Fresh Water Fish Commission, unpub. data). These activities stimulated a statewide food habits analysis that was based on collections of stomachs

obtained by trappers (Maehr and Brady 1986). In north Florida, Conner (1982) and Progulske (1982) examined population estimation techniques and movements, respectively. Foster (1992) described south Florida bobcat home range characteristics in conjunction with an evaluation of highway underpass effectiveness.

Papers detailing a variety of Florida black bear subjects span four decades. Like bobcats, most of these studies were conducted outside of south Florida, but they covered a greater diversity of topics. Although the greatest political issue following their listing in 1974 as a threatened species was sport hunting (Maehr and Wooding 1992), most black bear studies in the state have focused on basic natural history and bear/human conflicts. Compared to bobcats, black bears in Florida have been the subject of more work on diseases, parasites, and non-hunting management issues (Table 1.2).

In view of their rarity, Florida panthers have received an inordinate amount of scientific attention, with technical literature being published since 1950 (Table 1.2). Since then, publications on the basic natural history of this federal- and state-listed endangered subspecies have evolved into discussions of controversial issues ranging from property rights to genetic restoration. More than half of the published literature on Florida panthers appeared after 1990, so few generalizations can be made about the panther's historical distribution. There remain few unstudied aspects of the modern panther's biology or ecology, however, recent management has consisted of sporadic efforts to treat symptoms associated with small population size, rather than addressing the basic reasons for their current status or necessary steps for restoration.

Relative to most other species of terrestrial vertebrates in Florida, panthers, black bears, and bobcats exist at low density. A high degree of dispersion has contributed to a

Table 1.2. Journal papers and academic theses on large terrestrial carnivores in Florida, 1950-1995.

Year	Author	Subject	Location[1]
		BOBCATS	
1980	Guenther	Social ecology	SC
1982	Conner	Abundance estimation	N
1982	Progulske	Home range, habitat use	N
1982	Wassmer	Demographics, movements	SC
1982	Winegarner and Winegarner	Reproduction	SC
1985a	Winegarner	Field sign	SC
1985b	Winegarner	Den use	SC
1986	Maehr and Brady	Food habits	F
1988	Wassmer et al.	General ecology	SC
1990	Regan and Maehr	Melanism	S,SC
1992	Foster	Home range	S
1993	McLaughlin et al.	Parasites	F
		BLACK BEARS	
1961	Harlow	Status	F
1962	Harlow	Morphometrics	F
1968	Stafford and Williams	Capture technique	N
1974	Schemnitz	Distribution and abundance	S
1982	Brady and Maehr	Bee depredation	N
1982	Maehr	Electric fence design	F
1982a	Maehr and Brady	Beekeeper survey	F
1982b	Maehr and Brady	Fall food habits	N
1983	Conti et al.	Parasites	F
1984	Maehr	Seed dispersal	F
1984a	Maehr and Brady	Food habits	F
1984b	Maehr and Brady	Food habits comparison	N
1985	Brady and Maehr	Distribution	F
1985	Maehr and DeFazio	Foods	F
1986	Pirtle et al.	Diseases	N
1987	Wooding and Brady	Highway mortality	F
1988	Maehr et al.	Dispersal	S,SC
1989	Mykytka and Pelton	Home range and movements	N
1990	Mykytka and Pelton	Habitat use	N
1992	Wooding et al.	Movements	N
1992	Wooding and Hardisky	Denning	NC
1993	Forrester et al.	Parasites	N

[1] Letters refer to regions of the state: C=Central, F=Statewide, N=North, S=South, SC=South central.

Table 2. (continued)

Year	Author	Subject	Location
		FLORIDA PANTHERS	
1950	Allen	Vocalizations	S
1974	Schemnitz	Distribution and abundance	S
1980	Belden and Forrester	Description of specimen	S
1984	Johnson et al.	Identification	S
1985	Forrester et al.	Parasites	S
1988	Belden et al.	Habitat use	S
1988	Layne and Wassmer	Highlands County records	SC
1988	Roof and Maehr	Field sign survey	S,SC
1989	Greiner et al.	Parasites	S
1989a	Maehr et al.	Maternal behavior	S
1989b	Maehr et al.	Reproduction	S
1989c	Maehr et al.	Prey augmentation	S
1990	Harris	Genetics/geography	S
1990	Maehr	Private land conservation	S,SC
1990a	Maehr et al.	Food habits	S
1990b	Maehr et al.	Activity/denning	S
1990	McCown et al.	Capture technique	S
1990	O'Brien et al.	Genetics	S
1991	Bass and Maehr	Extirpation	S
1991a	Maehr et al.	Social ecology	S
1991b	Maehr et al.	Mortality	S
1991	McCown et al.	Deer condition	S
1991	Schortemeyer et al.	Management	S
1992	Maehr and Moore	Mass growth	S
1992	Maehr et al.	Home range	SC
1993	Belden and Hagedorn	Reintroduction feasibility	N
1993	Land et al.	Deer mortality	S
1993a	Roelke et al.	Genetics	S
1993b	Roelke et al.	Disease	S
1994	Barrone et al.	Reproduction	S
1994	Glass et al.	Disease	S
1995	Maehr and Caddick	Genetics/demographics	S
1995	Maehr and Cox	Landscape analysis	S,SC
1995	Maehr et al.	Parasites	S

low frequency of epizootics, although individuals of all three species are susceptible to a number of diseases, and Florida bobcat populations are known to have suffered locally severe disease outbreaks (Wassmer et al. 1988, Progulske 1982). An examination of disease occurrence in these species (Forrester 1992) suggests an inverse relation between body size and likelihood of disease. Bobcats have experienced temporary, local extinctions, while black bears appear relatively disease-free.

Because a spatially influenced resistance to disease may improve the survival probabilities of large, solitary carnivores, this same characteristic makes them vulnerable to habitat fragmentation and habitat loss. Maehr (1990) argued that it may be pragmatic to satisfy the habitat requirements of many species by meeting the spatial needs of a single species. The biological rationale for this approach has been debated (Wilson 1987, Terborgh 1988), but given their track records, it is unreasonable to expect natural resource agencies, which are traditionally underfunded and often unwilling to address multi-species management, to address the needs of the many wildlife species that are suffering the effects of range constriction. Thus, single-species, or trophic-level management remains as the substitute for a landscape-level approach to biodiversity conservation.

Harris and Cropper (in press) suggested that a combination of sea level rise, climate change, and anthropogenic influences have led to the post-Pleistocene faunal collapse that has occurred in Florida. Assuming that current rates of sea level rise will continue, it is clear that Florida's most widespread populations of panthers, black bears, and bobcats may also be its species most at risk. The displacement of tropical plant

communities and the elimination of large tracts of forest may negate landscape conservation efforts even if they were successful in the short term.

Study Area

It is ironic that while the development of south Florida is generally equated with the southeast coast, the earliest landscape-altering changes caused by humans occurred in southwest Florida. These changes began after passage of the Swamp Lands Act of 1850; legislation that was intended to stimulate the reclamation of inundated federal lands of the United States (Carter 1974). Inroads into the interior of south Florida began with the dredging of the Caloosahatchee River from the Gulf of Mexico to Lake Okeechobee. This water course, which originally began west of the lake near LaBelle, FL, drained the landscape on either side of the Hendry/Glades county line but left an upland linkage between southwest and south central Florida near Lake Okeechobee (Fig. 1.1). Although railroads had reached Miami by 1898 (Carter 1974), the modern vision of a drained and productive Everglades did not materialize until the campaign of Governor Napoleon Bonaparte Broward in 1904. The first canal to connect the Atlantic Ocean with Lake Okeechobee was dredged in 1906. This led to booming, and sometimes fraudulent, farmland marketing that hinged upon south Florida's rich muck soils. By 1929 over 730 km of canals aimed at draining the Everglades were in place. Clearing for farmland resulted in the elimination of a vast forest of custard apple (Annona glabra), a landscape feature of Lake Okeechobee's south rim that once hid Seminole Indians from Union troops, and likely facilitated the east-west movements of many species of south Florida's vertebrate wildlife. As human access to the lake increased, and roads and railways were

built as far south as Miami, construction began on the Tamiami Trail. Just as the dredging of east-west canals did for ships, this highway linked the east and west coasts for automobiles in 1928 and opened the Big Cypress Swamp to development.

With agriculture dominating much of the drainable wetlands and farmable uplands south of the Caloosahatchee River, some land preservation in south Florida had to be initiated. Everglades National Park and Collier-Seminole State Park were established in 1947, and Corkscrew Swamp Sanctuary was dedicated in 1954. Through the second half of this century the interplay between land preservation and land development became a chess match whereby each advance in creating a new preserve was countered with a new farm, pasture, or housing development. For example, before the Fakahatchee Strand could come under state ownership, all of its merchantable timber, primarily large cypress (Taxodium distichum) was removed by Lee Tidewater Cypress Company after the construction of an extensive network of elevated railroad beds, and its closed canopy forest was returned to an early successional stage (Burns 1984). Although the majority (9920 ha) of the strand was acquired by the state of Florida in 1974, 18,522 ha bordering the new preserve were marketed by Gulf American Land Corporation as an expansive residential development known as Golden Gate Estates. An intricate network of roads and canals, built to accommodate residents who may never construct homes, has now left an indelible mark on this part of the south Florida landscape. Controversy surrounding the construction of a regional jetport in western Dade County during the late 1960s and early 1970s resulted in a state-sponsored land purchase that was second in size only to Everglades National Park. The 230,770 ha Big Cypress National Preserve was established

by Act of Congress in 1974 in order to conserve natural resources and recreational opportunities. Approximately two decades transpired before the next significant wave of additions to conservation lands occurred in south Florida. In the meantime, the human population of Collier County more than doubled in each of the decades starting with 1960, 1970, and 1980 (Fernald and Purdum 1992), and Alligator Alley (the precursor to Interstate 75) was built to serve as the second high-speed roadway to connect the southeast and southwest coasts. The 10,120 ha Florida Panther National Wildlife Refuge was created in 1989, and over 40,000 ha are scheduled to be added to the Big Cypress National Preserve as the result of an unprecedented land swap between the private sector and the federal government (Maehr 1992).

As of 1990, over 1.4×10^6 ha in south Florida were held in public ownership (Fig. 1.1) and dedicated to conservation purposes (Maehr 1990). On the surface this appears to be a significant portion of south Florida under government stewardship, and indeed, nearly 60% of Collier County alone is in some form of government protection (which has led many local officials and community leaders to proclaim that no more land-saving actions are necessary). However, the vast majority of government land in south Florida is not conducive to agriculture nor urban development because of harsh soil and/or hydrological conditions (Leighty et al. 1954). In contrast to Collier County, neighboring Hendry County withstood a conversion between 1900 and 1973 of over 50% of its native cover to agricultural and urban uses (DeBellevue 1976). In the 23 years since then, south Florida has sustained continued increases in citrus, cattle production, sugar cane, and other agricultural land uses (Fernald and Purdum 1992) that, when combined with the dredging

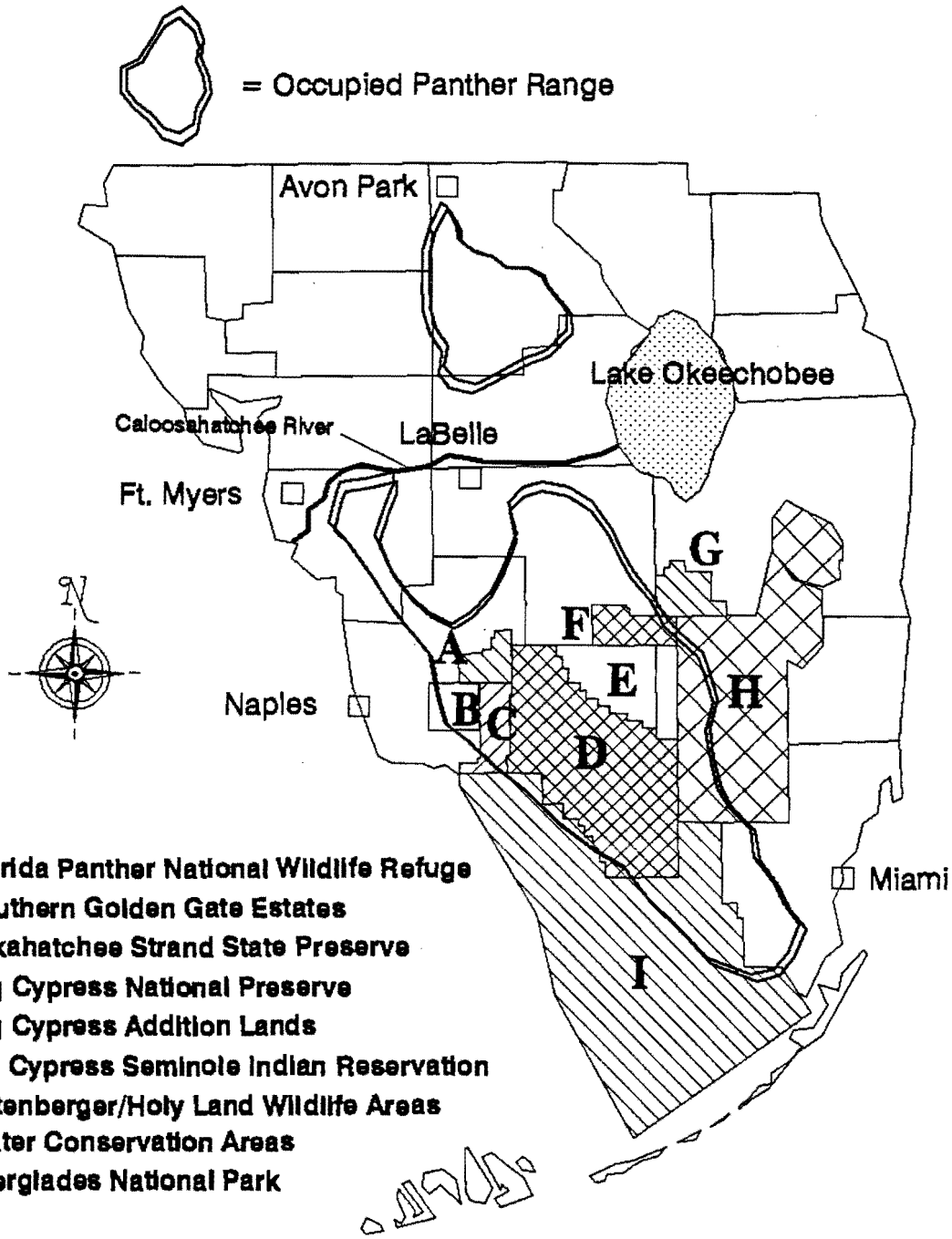


Figure 1.1. Study area and large tracts of publicly owned land in south Florida.

of the Caloosahatchee River, the clearing of the Lake Okeechobee custard apple forest, highway construction, and the impounding of much of the Everglades, have effectively isolated the forests of south Florida from the rest of the state.

The Natural Landscape

Although it lacks topographic relief, south Florida supports many recognized vegetation communities. The South Florida Water Management District lists 27 cover types in south Florida, while Myers and Ewel (1990) categorized 12 broad ecosystem types. The Soil Conservation Service (1981) described 26 ecological communities in Florida with 15 occurring in south Florida. McPherson (1984) listed six plant associations in the Big Cypress Swamp, while Olmstead and Loope (1984) recognized nine communities just in the Everglades. Craighead (1971) divided the vegetation of south Florida into nine provinces containing at least 45 distinct plant associations. The high variability inherent in south Florida vegetation communities results in part from the many zones of transition from one community to another, as well as the interests of the authors. Gradations between plant communities are also suggestive of the constant changes in species composition that have been, and continue to be, influenced by climate. The implications of this slow but inexorable landscape process is that vast expanses are necessary to accommodate not only the peregrinations of wildlife populations, but also the migration of plants and entire vegetative communities. Florida is considered more at risk from sea level rise due to global warming than is any other state (Henry et al. 1994), and south Florida has experienced more subsidence and consolidation of soils than any other region of the state. Effects of recent increases in salinity were observed in Everglades

National Park by Craighead (1971), and have had negative consequences on a variety of economically valuable environmental resources. Although sea level is not expected to rise beyond 65 cm by the year 2100 (Henry et al. 1994), even a change of this magnitude will cause widespread constrictions to the distribution of cover types that are important to the terrestrial vertebrate carnivores of south Florida.

Although south Florida lies within the Great Desert Belt of the earth (Henry et al. 1994), its climate is classified as tropical savannah (Koppen 1931: cited in Robertson 1955, Hela 1952), and monsoon rainforest (Trewartha 1943). A distinct warm wet season is typical from May through October when 60-80% of the annual average 1,525 mm of rainfall occurs (Craighead 1971). The mean annual temperature is 23 C with extremes of -2 C to 38 C (Duever et al. 1986). Southern Florida is often spared the effects of continental winter cold fronts due to the influence of warm air originating from over the Gulf of Mexico and the Caribbean (Henry et al. 1994). This has permitted the existence of a high diversity of tropical plants including palms, epiphytic orchids, and bromeliads. Topography is generally flat with most land laying below 7.6 m above mean sea level (Wade et al. 1980). Floods, fires, freezes, and droughts are considered to be the most important natural environmental influences on the distribution and kinds of plants in south Florida (Robertson 1955, Craighead 1971, Wade et al. 1980). Most non-anthropogenic fires are caused by lightning strikes associated with summer thunderstorms.

Davis (1943) assembled the most exhaustive account of vegetation communities in south Florida. Although he used only 9 broad categories, these were further divided into 64 subclasses. This classification was used as the basis for descriptions of bobcat, black

bear, and Florida panther habitat use and home range composition. Several of the communities that were described by Davis (1943) were combined in order to match a current observer's ability to correctly identify plant communities from 152 m elevation in a fixed-wing aircraft. For example, the subtle differences among 'oak and cabbage palm hammocks', 'cabbage palm hammocks', and 'low hammocks' were not consistently discernible from a fixed-wing airplane; nor are they remarkably different even at ground level. Other groupings were not used because they were unique to southeast Florida or they were not found in the study area. This resulted in the use of only 11 cover types for delineating the habitats of southwest Florida terrestrial carnivores. These are given on the following pages.

Pine flatwoods are dominated by slash pines (*Pinus elliottii*) growing in open forests on moderately well-drained soils. Saw palmetto (*Serenoa repens*) is a common and often dominating understory shrub.

Pine and cabbage palm woods are relatively limited in distribution and contain slash pine and cabbage palm (*Sabal palmetto*) in similar abundance. Saw palmetto is usually absent from this community.

Pine scrub is dominated by sand pine (*Pinus clausa*) with thickets of scrub oaks (*Quercus* spp.) and other xeric shrubs.

Hardwood hammocks are found on well- to poorly-drained soils and are dominated by broad-leaved deciduous oaks in association with cabbage palm and many temperate and tropical shrubs.

Mixed swamps are inundated forests of hardwoods such as red maple (Acer rubrum) and laurel oak (Quercus laurefolia) with cypress present but not dominant. Standing water can persist for a few months to the entire year depending upon drainage conditions and rainfall patterns.

Thicket swamps are shrub forests dominated by elderberry (Sambucus canadensis), willow (Salix caroliniana), pop ash (Fraxinus caroliniana), wax myrtle (Myrica cerifera), or buttonbush (Cephalanthus occidentalis). These areas are usually transition zones between swamp forests and marshlands and often occur following clearing or the abandonment of agricultural lands.

Bay tree forests are composed of broad-leaved evergreen trees including red bay (Persea borbonia), sweet bay (Magnolia virginiana), and dahoon (Ilex cassine) on poorly drained soils, and primarily in Highlands and Glades counties.

Freshwater marshes are treeless wetlands dominated by sawgrass (Cladium jamaicensis), flags (Thalia geniculata, Sagittaria spp., and Pontederia spp.) or wetland grasses and sedges.

Mangroves are found in coastal estuaries in saline to brackish water and are composed of red mangrove (Rhizophora mangle), black mangrove (Avicennia germinans), and white mangrove (Laguncularia racemosa). These species are usually divided into distinct zones with buttonwood (Conocarpus erectus) inhabiting the inner-most high salinity zone.

Agricultural/disturbed areas were once occupied by vegetation as described above but have been converted to croplands, improved pasture, rock mines, urban areas, and roadsides.

Summary of Previous Large Carnivore Work in Florida

Until the middle of the 20th century, most published literature on or relevant to Florida's large terrestrial carnivores dealt with general distribution, taxonomy, or economic status (Merriam 1896, Bangs 1898, Hamilton 1941, Young and Goldman 1946, Young 1946). Recent studies have focused more on biological, management, and conservation topics (Anderson 1983, Anderson 1987, Eagar and Stafford 1974, Pelton 1982, Tumilson et al. 1982).

Bobcat

Descriptions from Florida are similar to those from other parts of the bobcat's range: it is a secretive, solitary carnivore that specializes on small prey--especially rabbits, rodents, and to a lesser extent, birds. Maehr and Brady (1986) analyzed food habits throughout Florida and determined that there were no sex-related food preferences, but that seasonal variation in diet involved an increased use of artiodactyls and birds during fall and winter, respectively. The increase in use of birds is apparently in response to increases in over-wintering populations of migrants. Land et al. (1993) and Wassmer et al. (1988) reported similar proportions of prey species in bobcat diets from southwest and south central Florida; however, neither study revealed statistically significant seasonal variation. From a range-wide perspective, Florida bobcats utilize deer less frequently and birds more frequently than bobcats from other regions.

Wassmer (1982) and Guenther (1980) in south central Florida, and Foster (1992) in southwest Florida found that annual home range size ranged from 11.6 to 31.1 km^2 for adult males, and 5.8 to 21.6 km^2 for adult females. Progulske (1982) reported a mean of 44.4 km^2 for two adult male bobcats in north Florida. Florida bobcat home range sizes fall well within the extremes reported for the species (Foster 1992).

Bobcats in south central Florida preferred dense forest cover in an uplands-dominated landscape matrix (Wassmer 1988). Foster (1992) hypothesized that bobcats in southwest Florida preferred upland habitats although she did not compare frequency of use to habitat availability. Female bobcats appear to prefer thickets of saw palmetto for their natal dens (Wassmer 1982, Foster 1992). Winegarner (1985a) documented a bobcat natal den in a gopher tortoise burrow located in a dense saw palmetto thicket.

Foster (1992) reported considerable overlap among adult male bobcat home ranges in southwest Florida, but little overlap among adult females. Wassmer et al. (1988) recognized similar patterns in south central Florida. Both studies reported extensive overlap between males and females, and Wassmer et al. (1988) described a pattern of home range replacement and social ecology resembling the land tenure system described by Seidensticker et al. (1973) for mountain lions.

Reproductive characteristics have been described only as isolated anecdotes referring to a few individuals (Winegarner 1985a, 1985b, Winegarner and Winegarner 1982, Foster 1992) and for a local population in Highlands County (Wassmer et al. 1988). Based on these observations, litter size in Florida averages between two and three.

Most reports of mortality cite natural causes. Foster (1992) found that most of the study animals in southwest Florida avoided paved roads, and thus, avoided highway collisions. Wassmer et al. (1988) and Progulske (1982) found that disease was the major cause of death in south central and north Florida bobcat populations.

Although no statewide population estimates have been made, the Florida Game and Fresh Water Fish Commission considers bobcats sufficiently abundant to allow hunting and trapping throughout the state. Bobcats are likely still found in every county of Florida.

Black Bear

The black bear is Florida's largest terrestrial mammal, and it exhibits patterns of behavior and ecology that are typical of the species throughout North America. Early studies by Harlow (1961, 1962a) summarized body measurements that suggested black bears from Florida were as large or larger than individuals from northern populations. Schemnitz (1974) estimated a south Florida population of 145, while Harlow (1962b) estimated that 800-1000 inhabited the entire state.

The earliest telemetry studies occurred in north central Florida in response to concerns over proposed phosphate mining in Osceola National Forest (U.S. Dept. Interior 1979). This study resulted in an evaluation of home range estimation techniques (Mykytka and Pelton 1989), and a habitat analysis that suggested the importance of large swamps and pine flatwoods ecosystems (Mykytka and Pelton 1990). Osceola National Forest home ranges of two females were 93.4 and 39.4 km^2, while six males ranged from

35.9 to 457.2 km^2 (X=171.1 km^2). Wooding and Hardisky (1988) estimated male and female black bear home ranges in Ocala National Forest at 170 and 26 km^2, respectively.

The black bear's ability to tolerate anthropogenic alterations to the landscape is reflected in its widespread contemporary distribution (Maehr 1984, Brady and Maehr 1985), as well as the statewide bee hive-depredation problem (Maehr 1982, Brady and Maehr 1982, Maehr and Brady 1982a). Although such interactions may lead to bear poaching, highway collisions are the most common form of human-related mortality (Wooding and Brady 1987). Natural mortality has been documented infrequently but may include occasional predation by Florida panthers (Maehr et al. 1990a) and cannibalism (Wooding and Hardisky 1988). Black bears are susceptible to a variety of diseases and parasites (Conti et al. 1983, Pirtle et al. 1986, McLaughlin et al. 1993), but none have been demonstrated to be a significant mortality factor (Forrester 1992).

Food habits have been examined from statewide and regional perspectives. Maehr and Brady (1984a) measured seasonal changes that are consistent with findings from other parts of the species' range. Food availability and diversity vary geographically (Maehr and Brady 1982b, Maehr and Brady 1984b), and are composed primarily of fruits and insects (Maehr and DeFazio 1985), but Florida black bears also feed opportunistically on a variety of vertebrates.

Like their North American conspecifics, black bears in the Ocala National Forest exhibit seasonal movement patterns (Wooding and Hardisky 1988). While some males remain active throughout the year, restricted movements during winter are particularly pronounced among pregnant females.

Although black bears were listed by the state of Florida as threatened in 1974 (Maehr and Wooding 1992), fall and winter hunting were permitted in Apalachicola National Forest and Baker and Columbia counties until 1994 when an experimental moratorium was imposed. Although the species was recently documented in at least 50 of Florida's 67 counties (Brady and Maehr 1985), its distribution is almost exclusively confined to five disjunct populations. Occasional long-distance dispersal movements (Maehr et al. 1988) have the potential to occasionally cross the gulfs between some of these populations.

Florida Panther

The existence of the Florida panther was debated for several decades until its "official" rediscovery in 1973 by Nowak and McBride (1973), who estimated the south Florida population at 20-30 individuals. Although evidence of panthers has continued to emanate from south central Florida (Layne and Wassmer 1988, Maehr et al. 1992, Maehr 1994) and the St. Johns River drainage (Maehr 1992), concerted research efforts have been restricted to south Florida. Prior to the capture of an old female in Glades County in 1973 (Nowak and McBride 1973), the south Florida population was estimated to be 92 (Schemnitz 1974). Williams (1978) placed the population at 30-50 individuals, and stated that credible but unsupported sign originated only from Collier County. Roof and Maehr (1988) developed a standardized survey method for field verification of panther sign. Based on such sign surveys and extrapolations from radio-collared study animals, the contemporary population in southwest Florida (exclusive of the Everglades and eastern Big Cypress Swamp) is estimated at 70-80 individuals (Maehr et al. 1991a).

Young and Goldman (1946) described the Florida subspecies and its distribution in the southeastern United States. Allen (1950) discussed vocalizations of captive panthers, and a specimen examined by Belden and Forrester (1980) solidified the stereotypic description of the modern subspecies- especially the characteristic crook at the end of the tail, and a whorl of dorsal hair near the scapulae. Similarities between some panther and bobcat scats (feces) led to an unsuccessful effort to differentiate the two species with chromatographic bile assays (Johnson et al. 1984).

Specialized capture techniques (McCown et al. 1990) have been a part of intensive and invasive examinations of individual panthers during anesthesia and necropsies since the mid-1980s. As a result, a detailed catalog of parasites (Forrester et al. 1985, Greiner et al. 1989, Maehr et al. 1995) and diseases (Forrester 1992, Roelke et al. 1993b, Glass et al. 1994) has been assembled. Although no parasites have been demonstrated to be pathogenic, Notoedric mange has the potential to cause mortality at least in juveniles (Maehr et al. 1995). Diseases that have caused mortality include bacterial infections, rabies (Roelke et al. 1993b), and pseudorabies (Glass et al. 1994). Mortality caused by highway collision is well documented but is less important to the wild population than natural mortality- especially within species aggression (Maehr et al 1991b). Illegal killing has not been documented for over a decade and capture-related deaths are rare.

Panthers prefer native uplands over other habitat types in south Florida (Belden et al. 1988, Maehr et al. 1991a, Maehr et al. 1992). Maehr and Cox (1995) found that large patches of forest cover were important in explaining panther occurrence and that natural and unnatural habitat fragmentation reduced the value of these forests to panthers.

Thickets of saw palmetto are important as daytime rest sites and natal dens (Maehr et al. 1990b). Age at first reproduction in females is 18 months (Maehr et al. 1989b) and males have not been observed to breed before three years of age (Maehr et al. 1991a). Average litter size is 2.25 (Maehr and Caddick 1995) and births have occurred in almost every month. Survival of kittens between birth and 12 months of age is greater than 0.80 (Maehr and Caddick 1995), and annual mortality of all sex and age classes combined is less than 0.20 (Maehr et al. 1991b).

Florida panthers exhibit a system of land tenure typical of solitary carnivores (Maehr et al. 1991a). Home ranges averaged 519 km^2 and 193 km^2 for adult males and adult females, respectively. Activity of both solitary and denning panthers follows a bimodal pattern with crepuscular peaks (Maehr et al 1990b). Female panthers exhibit a regular pattern of den attendance during the two months that kittens are unable to travel (Maehr et al. 1989a). Litter size appears to be a function of prey abundance and habitat productivity . Attempts to artificially augment prey availability were unsuccessful (Maehr et al. 1989c).

Concerns over nutritional status led to a preliminary conclusion that female panthers were consistently undernourished and anemic (Roelke et al. 1985). However, food habits analyses indicated that prey abundance and distribution varied geographically (Maehr et al 1990a). Panther prey in south Florida follows a northwest to southeast gradient of declining abundance (McCown et al 1991) that appears to be a product of soil and primary productivity. Wild hogs (Sus scrofa) are the most frequently taken prey, however, this species is sparse south of Interstate 75. White-tailed deer (Odocoileus

virginianus) and wild hogs combined account for 70% of the frequency of occurrence in panther scats. Where both species are abundant (i.e. the north part of the range), panthers are larger, more abundant, and produce more kittens. This led Maehr (1990) to emphasize the importance of private lands in Collier and Hendry counties to the future of the subspecies.

At least some rationales argue that low numbers increase the extinction probabilities for small populations. In addition to demographic stochasticity and unpredictable climatic events, genetic problems have been suggested as a primary threat to panthers (Roelke et al. 1993a). O'Brien et al. (1990) identified two distinct lineages of wild panthers in south Florida- one originating in situ, the other originating from captivity. Despite this apparent introgression, they concluded that the south Florida population was suffering from reduced allozyme variation when compared to other cougar populations. Spermatozoa abnormalities (Barrone et al. 1994), heart defects, infectious diseases, and matings between close relatives (Roelke et al. 1993a) have been suggested as symptoms of a collapsing population. However, Maehr and Caddick (1995) reminded that philopatry is expected in a land tenure social system, and thus, matings between close relatives, especially males and their female offspring, are typical. O'Brien et al. (1990) led Harris (1990) to point out that the reason for the genetic variation documented in south Florida may date to the Pleistocene connection between Florida and the Yucatan Peninsula. Regardless of the panther's lineage in south Florida, normal demographics as indicated by behavior typical of the species, low mortality, high natality and kitten survival, may be indicative of a high level of local adaptation. These factors may be ameliorating the effects

of small population size and reducing the potential for genetic problems to be immediate conservation concerns (Maehr and Caddick 1995).

General Methodology

The data upon which this dissertation is based were collected primarily while I was the supervisor of research for the Florida Game and Fresh Water Fish Commission in south Florida from 1985-1994. Field activities focused primarily on Florida panther captures and the monitoring of their radio collar signals. This work began in 1981 and continues to this day. Methods of panther capture and restraint have been described in detail by McCown et al. (1990) and Barrone et al. (1994). Bobcats were captured opportunistically primarily during 1986 and 1987 when panther hunting with hounds trained to trail and tree cats. Bobcats were handled in a fashion similar to panthers, but due to their smaller size, they were fitted with smaller radio collars with functional lives of no more than a year. Black bears were captured with Aldrich spring-activated snares and with culvert traps primarily during the three-year span, 1991-1993. Bears were anesthetized using Ketamine hydrochloride at a dosage of 20mg/kg and administered with a pole syringe. Radio collars worn by adult black bears and adult panthers had battery lives of at least two years. Florida panthers were captured as necessary to replace aging transmitter batteries and maintain contact with study animals.

All study animals were regularly monitored from fixed-wing aircraft at an altitude of about 150 m following the methodology of Mech (1983). Florida panthers were located three times per week, black bears were located three times every two weeks, and bobcats were located approximately once each week. Location data included Universal

Transverse Mercator coordinates, habitat type, time of day, animal identification number, and an index to activity if the study animal carried a transmitter that contained a motion-sensitive switch (Telonics, Inc., Mesa, AZ). Additional telemetry data used in these analyses for panthers monitored by the National Park Service or following the termination of my involvement with field activities were obtained through requests to the Florida Game and Fresh Water Fish Commission's Office of Environmental Services. More specific field methods and the statistical analyses used are described in detail within subsequent chapters.

CHAPTER 2

DIETARY OVERLAP

Although the actual nutritional requirements of most wildlife species are unknown, food remains the most commonly examined resource for assessing the degree of interspecific competition (Hutchinson 1957, Caughley and Sinclair 1994). The food habits of native large terrestrial carnivores in Florida have been well-described (Maehr and Brady 1982, 1984a, 1984b, Maehr and DeFazio 1985, Maehr and Brady 1986, Maehr et al. 1990, Wassmer et al. 1988). However, they have not been examined for potential dietary overlap. Further, published food habits data are primarily from north Florida for black bears, south central Florida for bobcats, and from south Florida for panthers. Black bears in north Florida exhibit only modest differences in food habits (Maehr and Brady 1984b), and bobcat diets in south Florida are similar to those reported for the entire state (Land et al. 1993). I examined previously published data for bobcats and Florida panther food habits, and compared these with unpublished food data for black bears in south Florida.

Methods

Collection, identification, and analytical procedures for foods of bobcats and panthers can be found in Maehr and Brady (1986), and Maehr et al. (1990). Because

volumetric measurements were made for contents of bobcat stomachs, these data were converted to percent frequency in order to allow for direct comparisons with other species. Black bear scats were collected throughout south Florida at trap sites and during routine field activities associated with radio telemetry studies. Scats were rinsed with water through a 1 mm sieve and individual food items were separated in a white enamel wash pan. Reference collections and guides (Martin and Barkley 1961, Schopmeyer 1974, Tomlinson 1980, Arnett 1985) were used to identify foods as close to species as possible. Black bear foods were then examined by month in order to detect seasonal patterns related to food availability or preference. These patterns formed the basis for seasonal comparisons among the three native large carnivores in south Florida.

Although the possibility for gender-related differences in diet exists, Maehr and Brady (1986) found that male and female bobcats had similar food habits, Anderson (1983) did not report sex-related differences in cougar diets, and Schwartz and Franzmann (1991) found that black bears exhibited no sex-related differences in rate of moose calf (Alces alces) predation. Therefore, gender was ignored in comparisons of diets. Sorenson's similarity coefficient (Greig-Smith 1964) was used to quantify the amount of annual dietary similarity between bears, bobcats, and panthers using species occurrence data from Maehr et al. (1990), Land et al. (1993), and this study. Dietary overlap between species was estimated by using Pianka's (1986) variation of an algorithm first presented by MacArthur and Levins (1967):

$$O_{jk} = \frac{\sum_j P_{ij} P_{ik}}{\sqrt{\sum_j P^2_{ij} \sum_j P^2_{ik}}}$$

where P_i is the proportion of food resource in the $_i$th species class, and n is the total number of species categories. O_{jk} then, has a possible range of values from 0 to 1. Higher values equate to higher levels of overlap. Shannon-Weiner indices of diversity (Shannon and Weaver 1963) were calculated using percent frequency of foods. Because not all cited studies identified small mammals, birds, and lagomorphs to species, these items were grouped into three categories.

Nutritional analyses were conducted on selected black bear foods that were frequently consumed in south Florida. Food items were collected in occupied black bear range in south Florida, oven-dried at 60^0 C, then ground in a Wiley mill. Analyses conducted at the Forage Evaluation Support Laboratory, Animal Nutrition Lab, University of Florida, Gainesville measured dry matter, organic matter, total neutral-detergent fiber, ash-free neutral-detergent fiber, total nitrogen, crude protein, in vitro organic matter digestibility, and total phosphorous. Crude fat was measured by A & L Plains Agricultural Laboratories, Inc., Lubbock, Texas, using ether extract methodology. Ants were washed, separated, and dried at 100^0C for 48 hours, and milled through a 1 mm screen at the Caesar Kleberg Wildlife Research Institute, Texas A and M University at Kingsville, Texas. Milled samples were dried again and two g aliquots of ground ants were extracted for eight hours with petroleum ether. Samples were dried again, weighed, ashed at 600^0 C for five hours, dried and weighed.

Results and Discussion

The three native carnivores in south Florida exhibited distinct trends in their utilization of important species or groups of species. Results of food habits studies from south Florida were comparable to the results of food habits studies of the same species in

Table 2.1. Comparison of food habits among south Florida's native large mammalian carnivores. Data summarized from Maehr and Brady 1986[1], Land et al. 1993[2], Maehr et al. 1990a[3], Maehr and DeFazio 1985[4], and this study[5].

	SPECIES				
	Bobcat[1]	Bobcat[2]	Panther[3]	Black Bear[4]	Black bear[5]
Food type	Percent frequency in diet				
Rodents & insectivores	36	36	2	0	0
Lagomorphs	25	37	4	0	<1
Birds	16	14	<1	1	0
Opossum	1	0	0	0	0
Armadillo	0	0	8	1	<1
Raccoon	<1	7	12	0	0
W.t. deer	2	3	28	<1	<1
Black bear	0	0	<1	0	<1
Feral hog	1	0	42	<1	<1
Livestock	0	0	2	0	<1
Alligator	0	0	<1	<1	0
Other herps	<1	1	<1	<1	0
Insects	0	0	0	30	16
Plant fiber	11	--	--	6	27
Soft mast	0	0	0	22	23
Hard mast	0	0	0	25	30

more northern Florida locales (Table 2.1).

Bobcats

Maehr and Brady (1986) found that Florida bobcats specialized on small prey and killed white-tailed deer infrequently. Land et al. (1993) confirmed this general pattern for southwest Florida, although in their study of female deer mortality within the range of the Florida panther, bobcats killed more deer than did panthers. Maehr and Brady (1986) attributed bobcat consumption of deer to crippling and mortality caused by sport hunting, whereas Land et al. (1993) believed that predation on deer was caused by a small proportion of the local population occasionally ambushing prey in habitats that panthers generally avoided (i.e. freshwater marsh). Seasonal variation in Florida bobcat diets may be due to an influx of overwintering migrant birds, hunter harvest of large prey, and annual patterns in small prey reproduction (Maehr and Brady 1986). Much of south Florida is closed to doe hunting, and mild winters maintain food supplies for small mammals. Thus, hunter crippling/mortality, and annual fluctuations in small mammal abundance are likely of lesser influence to bobcat nutrition than the sometimes five-fold increases in over-wintering bird densities (Robertson and Kushlan 1974).

Florida Panthers

Maehr et al. (1990) found that Florida panthers specialized on large prey, especially wild hogs and white-tailed deer. Proportions of food items in the diet did not change seasonally, however, smaller prey such as raccoons were consumed in areas with low densities of large prey. These areas also support lower panther densities with only sporadic reproduction (see Maehr et al. 1989). In Everglades National Park where

panthers became effectively extinct in 1991 (Bass and Maehr 1991), panthers occasionally consumed river otters (Lutra canadensis), bobcats, and alligators (Alligator mississippiensis) (O.L. Bass, pers. comm.), apparently because preferred prey was limited (Smith and Bass 1994). Like populations of cougar throughout North America, Florida panthers seem inextricably tied to a resident deer population.

Black Bears

Despite the copious food habits data on Florida black bears, none of the studies was conducted in south Florida where tropical climate and seed sources have created a much different milieu than the habitats available to bears in central and north Florida. Analysis of 739 scats collected from July 1991 through 1993 indicated that black bears in south Florida consumed at least 40 species or distinct parts of plants, insects, and mammals. Several species including saw palmetto, cabbage palm, giant palm weevils (Rynchophorus cruentatus), and social insects provided at least two plant parts or life stages as food. Apical meristems and seeds were available on both of the palm species, whereas eggs, larvae, adults, and honey (when available) of colonial insects were eaten. Several species did not appear in scats but were observed to be eaten such as Florida damp-wood termites (Prorhinotermes simplex), or have been reported previously, for example, alligator eggs (Maehr and Brady 1984a).

Monthly analyses of food habits (Table 2.2) were used to separate the year into categories that corresponded to plant phenology and bear behavior related to denning (Fig. 2.1). This resulted in the subjective division of the year into three seasons; winter (January-April), summer (May-August), and fall (September-December). Winter foods

Table 2.2. Frequency of occurrence by month of foods eaten by black bears in south Florida 1991-1993. Numbers below months represent scats per month.

	Frequency of occurrence by month											
	J	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**
Species	80	14	8	12	78	27	44	25	72	131	110	138
Plant fibers												
Serenoa repens				1	1		9	4	19	6	4	3
Sabal palmetto	5			9	6	1	15	1	4	4	15	5
Pontederia cordata	11	2	2	3	14	1	11	2	2	6	11	16
Cladium jamaicense	2	1			36	7	2	1		1	2	
Thalia geniculata	16	2	1		1	1	7	5	3	14	16	33
Potamogeton spp.							1					
Cirsium horridulum					23							
Tilandsia spp.	2						1		3			2
Graminae	1	2			3					4		2
Unknown					1			4	2	5	2	7
Soft mast												
Psychotria nervosa				2						5	6	7
Psychotria sulzneri									1			
Lantana involucrata				1	9	16					1	
Vitis spp.								10	20	2		
Persea borbonia									3	8		1
Celtis laevigata										4	1	
Callicarpa americana									2	3		1
Ardisia escalloniodes	1											
Schinus terebinthefolius	67	8	2	1	1					2	31	65
Ilex cassine									4	5	2	
Cornus foemina							17	12	19	3	1	
Smilax spp.	1										1	
Rubus spp.					7	1						
Unknown										2		
Hard mast												
Serenoa repens		1		1		8	3	9	45	89	36	13
Sabal palmetto	14	1	1						3	36	77	74
Quercus spp.	1								1	4	16	31
Carya pallida									1			
Roystonea elata	1											

Table 2.2. (continued)

SPECIES	J	F	M	A	M	J	Ju	A	S	O	N	D
Insects												
Odontotaenius disjunctus	1				2	2	1		2	6		
Rynchophorus cruentatus	2						4	4	3	10		1
Polistes spp.									1	1		
Apis mellifera	3	3			1	1			3		2	
Xylocopa spp.	2			1	1		3	2	12	33	3	5
Campanotus floridanus				5	21	5	9	3	9	20	5	
Vespula squamosa	1				5		1		2	8	1	
Unknown Coleoptera					2	4	1		3		4	4
Cicadidae							1					
Unknown wasp					1				1	1		
Crematogaster pilosa	1			1			4		3	8		2
Unknown insect					1					1		2
Vertebrates												
Dasypus novemcinctus					1				2	3	1	
Odocoileus virginianus	3				1						2	3
Sus scrofa		1									3	
Ursus americanus			1						1			
Sylvilagus spp.					1	1				1		
Capra spp.									1			
Bone										1		2
Eggshell							1					
Human origin					1	6	2		1	2		

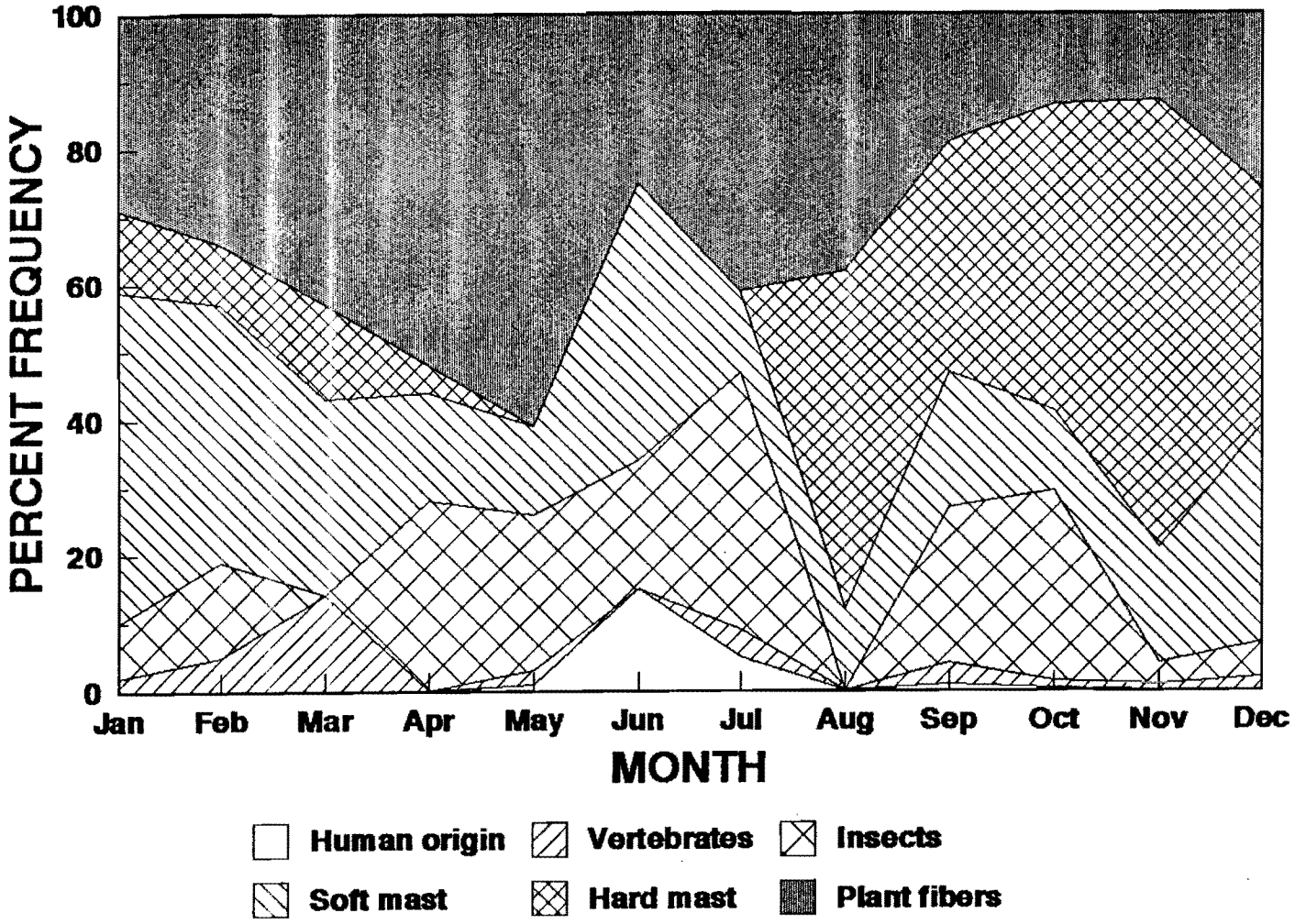


Figure 2.1. Temporal variation in black bear food consumption in southwest Florida from 1991-1993.

were characterized by a preponderance of soft mast, primarily the fruits of Brazilian pepper (Schinus terebinthefolius), and plant fibers such as alligator flag (Thalia geniculata), and pickerel weed (Pontederia cordata) (Table 2.3). Summer foods were dominated by plant fibers and insects, and included the fruit of swamp dogwood (Cornus foemina) and lantana (Lantana spp.). Swamp dogwood fruits are locally abundant and very high in crude fat relative to other plant foods (Table 2.4). Such high energy foods are unusual for this time of year in other parts of the black bear's range. Although summer and winter diets appear similar when only major categories are compared (Table 2.3), these two seasons are distinguished primarily because of the widespread availability of Brazilian pepper seeds in winter when few other seeds are available, and because ant consumption increases during May. In addition, lantana, which is a tropical genus that contains at least one native species as well as several naturalized forms (Nellis 1994:136), is available primarily during early summer (Fig. 2.2). Fall foods were mostly seeds of saw palmetto, cabbage palm, and to a lesser degree, live oak (Quercus virginiana). This seasonal pattern in food habits is similar to other descriptions of black bear food habits in the southeastern U.S. (Hardy 1974, Landers et al. 1979, Beeman and Pelton 1980, Eagle and Pelton 1983, Maehr and Brady 1984a, Smith 1985b, Garner 1986, Hellgren and Vaughan 1988), where an abundance of hard mast such as acorns follows a period of soft fruit availability, and precedes winter denning and hibernation. This period has been described as critical to determining reproductive output the following winter and mast failures have caused measurable impacts to cub production the following year (Rogers 1976). South Florida, however, has a strong tropical influence and has been invaded by a

Table 2.3. Seasonal changes in percent frequency of food types in south Florida black bear diets.

	Percent frequency					
Season	Plant fiber	Soft mast	Hard mast	Insects	Vertebrate	Artificial
Winter	42.6	25.9	7.4	18.5	5.5	0
Summer	47.6	22.5	3.4	22.5	1.4	2.5
Fall	19.4	20.1	42.6	15.5	2.1	0.3

Table 2.4. Nutrient composition of foods that account for 70.2 percent of the diet of black bears from south Florida.

Food Item	Part	% Diet	Crude protein	% Dry matter	% Total NDF[1]	Ash-free NDF	% Total N[2]	% Total P[3]	% Crude fat
Cabbage palm	Fruit	13.3	6.27	90.2	66.3	65.8	1.00	-	2.99
Saw palmetto	Fruit	12.7	4.92	89.0	48.3	46.4	0.78	0.119	9.42
Brazilian pepper	Fruit	11.5	7.30	93.0	36.2	35.6	1.16	0.219	10.28
Alligator flag	Fiber	6.4	18.02	88.9	40.3	39.3	2.88	-	0.85
Carpenter ant	Adult	5.0	-	-	-	-	-	-	11.68
Saw palmetto	Fiber	4.5	17.83	87.0	45.7	44.5	2.85	-	0.46
Cabbage palm	Fiber	4.5	19.69	87.6	28.9	27.6	3.15	-	1.99
Swamp dogwood	Fruit	3.4	6.13	95.2	54.6	52.3	0.97	0.168	17.16
Oak[4]	Fruit	3.4	5.90	-	18.7	23.8	-	-	4.30
Wild grape	Fruit	2.2	7.75	91.6	36.2	36.6	1.24	0.202	4.50
Thistle	Bloom	1.5	9.20	94.4	47.1	46.9	1.46	0.333	4.03
Deer[7]	Flesh	0.6	47.4	-	0	0	-	-	41.30
Arboreal ant[6]	Adult	1.2	-	-	-	-	-	-	45.45
Gallberry[5]	Fruit	0	4.90	-	12.8	-	-	-	3.40

[1]neutral-detergent fiber
[2]nitrogen
[3]phosphorus
[4]Short and Epps 1976
[5]Landers et al. 1979
[6]Crematogaster pilosa
[7]McCullogh and Ullrey 1983

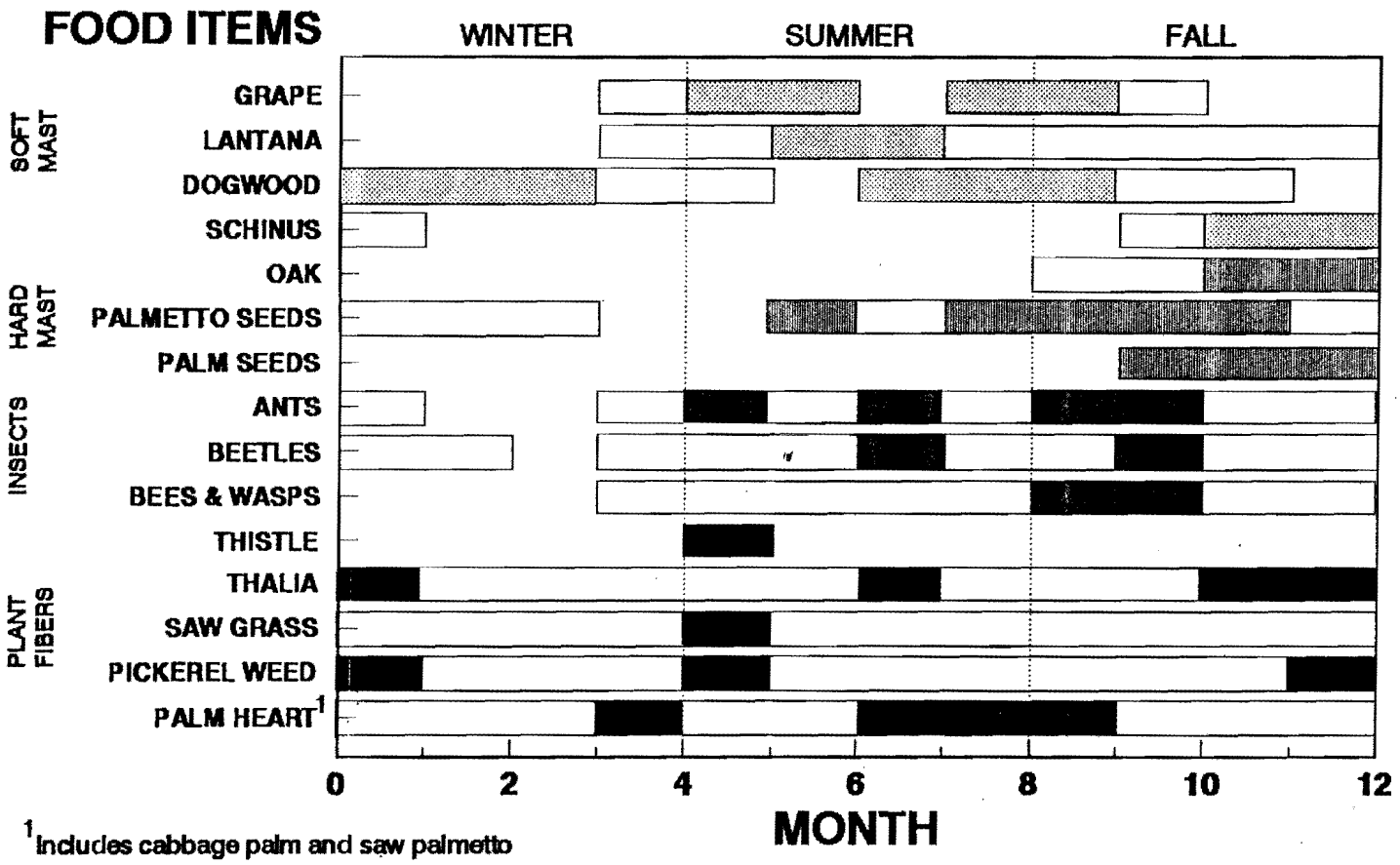


Figure 2.2. Availability of selected black bear foods in southwest Florida, 1991-1993. Horizontal bars represent months when the listed food item is available. Filled bars indicate the months when that food item is eaten by bears.

very abundant winter-fruiting exotic shrub (Brazilian pepper). Further, native plants such as saw palmetto and cabbage palm provide food year-round; a sharp contrast to nutritional opportunities for black bears in those parts of North America devoid of native palms and introduced, food-producing tropical shrubs.

This study recorded several food items that were previously unreported for black bears. These included sawgrass (Cladium jamaisence), bromeliads (Tillandsia spp.), thistle (Cirsium horridulum), marlberry (Ardisia escallonioides), royal palm (Roystonea elata), giant palm weevil, and a colonial semi-arboreal ant (Crematogaster pilosa). The first two of these new species may be important foods during times of limited soft and hard mast availability. The latter two are of interest because they are highly nutritious and involve adaptive feeding strategies.

Giant palm weevils feed and reproduce in damaged palms (Woodruff 1967), and I have frequently observed weevils colonizing recently damaged cabbage palms and palmettos throughout Collier County. The damage was caused by the deliberate extraction of the apical meristems for human consumption- an activity that mimics black bear feeding. Given that other palm-damaging forces are rare in south Florida (i.e. lightning and wind do not appear to damage either species), then the creation of feeding and egg-laying conditions for giant palm weevils may depend largely on the activities of humans and black bears. If these weevils benefit from the creation of feeding and egg-laying conditions, and black bears occasionally return to previously damaged plants and consume the weevils, then this may represent a symbiotic relation that hinges on south Florida's native palms. In other words, black bears are known to utilize "hearts-of-palm"

as foodstuff. The damaged palms apparently release a volatile pheromone-like compound that attracts palm weevils. Black bears that return to a palm or palmetto that they had previously fed upon are further rewarded by the availability of nutritious palm weevils.

The small, semi-arboreal ant, Crematogaster, builds wasp-like nests in shrubs and stout herbaceous vegetation in wet prairies and thicket swamps. While tracking radio-collared bears from aircraft, trails were visible in the marshes surrounding the Fakahatchee Strand, and individual bears were occasionally seen standing in open settings along these trails. Subsequent field investigations revealed that these trails were made by black bears venturing out of the dense mixed swamp forest in order to feed on these tiny (3-5 mm long), but abundant insects. Ether extract analyses indicated that the crude fat content of adult Crematogaster exceeds the fat content of white-tailed deer flesh (Table 2.4) and was nearly four times greater than the fat content of the commonly consumed Florida carpenter ant (Campanotus floridanus).

The availability of alternative high-energy foods may help explain the low frequency of mammalian prey in the diets of south Florida black bears compared to bears from other parts of the species' range. For example, Schwartz and Franzmann (1991) found that early summer diets of black bears in Alaska would provide insufficient nutrition without the frequent consumption of moose. Although Rogers (1987b) concluded that black bears specialize on plant foods because they are poor predators, their carnivore dentition still offers this alternative when animal prey are available. Although domestic livestock, wild hogs, and armadillos are common, noisy, and often unwary potential prey in south Florida, they were rarely consumed by bears. Thus, the year-round availability of

a variety of plant and insect foods (Table 2.3) may not only reduce potential conflict with livestock owners and apiarists, but may also reduce the likelihood for competition with bobcats and panthers.

Nutritional analyses of frequently consumed foods indicated that a high energy and moderate-protein diet can be maintained by black bears throughout the year without the consumption of vertebrates which are high in both crude fat and crude protein (Robbins 1983). In Florida 70% of panther and 51% of bobcat diets are composed of two species of mammals (Maehr and Brady 1986, Maehr et al. 1990). The ability of these cats to subsist on the much lower diversity diet is certainly a reflection of the constant availability of prey, which, in turn, reduces seasonal variation in home range use.

Most black bears in this study and elsewhere (Pelton 1982) exhibit extensive fall movements. Such movements appear to be a universal phenomenon that must precede denning, hibernation and successful overwintering in temperate North America. In south Florida however, most bears remain active through the winter and feed on a variety of fibrous plant material as well as Brazilian pepper, which is not only widely distributed throughout south Florida, but is also one of the highest energy plant foods anywhere in the black bear's range. South Florida black bears ate the apical meristems of palms and the vegetative parts of several emergent plants in every season. Although these species are low in fat and protein, they are highly digestible (in vitro organic matter digestibility=93.8% for cabbage palm heart, and 83.6% for Thalia), and there was always at least one abundant fruit available that was high in available energy. This year-round availability of plant and insect foods, many of which are high in lipid content, may also

help explain the rapid mass growth and early age of first reproduction that has been documented for south Florida black bears (see Appendix B).

Compared to black bears from north Florida, the fall diet in south Florida bears contains a considerably greater variety (Table 2.5). Maehr and Brady (1984b) suggested that saw palmetto fruit may not be preferred because bears in northwest Florida consumed black gum (Nyssa biflora) and odorless bayberry (Myrica inodora) with greater frequency when all three species were available. This may be true for a short period of time in north Florida inasmuch as Treichler et al.(1946), Bonner (1971), Short et al.(1975), and Hellgren and Vaughan (1988) found that the fruit of the closely related Nyssa sylvatica is higher in crude fat than is saw palmetto. However, north Florida food habits studies were conducted where black bears may have avoided upland habitats when hunter activity along roads was highest during the legal fall bear season. Further, the extensive home range shifts of radio-collared bears to areas of abundant saw palmetto (see home range chapter), and the dominance of its fruit in bear diets in this study suggest that saw palmetto fruit is in fact preferred in south Florida.

Avoidance of potential foods is suggested for gallberry (Ilex glabra), American beauty berry (Callicarpa americana), and Florida trema (Trema micrantha) inasmuch as these species are extremely common and widely distributed in south Florida black bear range, and yet they contribute little or nothing to the bear's diet. Although nutritional analyses were not conducted for these three species, Landers et al. (1979) found that gallberry was low in both protein and fat content. A similar phenomenon was found among north Florida bears where gallberry is very abundant, produces fruit regularly, but

was consumed relatively infrequently compared to species of higher nutritional quality (Maehr and Brady 1984a).

Species Comparisons

As similar lifestyles should predict, bobcats and panthers had more prey in common with each other than did either species with bears (0.57)(Table 2.6). In addition, the diets of both cat species were comparably diverse (Table 2.5). Black bears overlapped less than 0.20 with either bobcats or panthers and this overlap was almost totally due to the occasional consumption of armadillo, white-tailed deer, and wild hog flesh.

While the Sorenson similarity coefficient is useful as an index to prey species overlap among predators, it does not take into account the differential use of these foods. The Pianka algorithm also has its shortcomings, but it utilizes frequency of occurrence data and thus, from a potential competition perspective, is likely better for portraying the actual degree of resource-use overlap between species. These calculations suggest that even between cat species there is little food overlap among south Florida's native large terrestrial carnivores (Table 2.6, Fig. 2.3). The predatory lifestyle of black bears in south Florida appears to be purely opportunistic and is clearly demonstrated by Pianka overlap coefficients of less than 0.02 with both cat species. Similarly, the apparent overlap between panthers and bobcats was diminished when frequency of occurrence was considered. Whereas black bears are known to inflict considerable mortality on some populations of large ungulates in other regions (Behrend and Sage 1974, Franzmann et al. 1980, Ozoga and Verme 1982, Verspoor 1983, Wilton 1983, Franzmann and Schwartz 1986, Matthews and Porter 1988), as are bobcats (Hamilton and Hunter 1939, Pollack

Table 2.5. Diversity of large native terrestrial carnivore diets in Florida.

Species	Location	Reference	Annual H'	Fall H'
Florida panther	Southwest Florida	Maehr et al. 1990	1.51	-
Bobcat	South central Florida	Wassmer et al. 1988	1.88	-
Bobcat	Southwest Florida	Land et al. 1993	1.39	-
Bobcat	North Florida	Maehr and Brady 1986	1.51	-
Black bear	South Florida	This study	3.00	2.60
Black bear	Northeast Florida	Maehr and Brady 1982	-	1.49
Black bear	Northwest Florida	Maehr and Brady 1984b	-	1.69

Table 2.6. Dietary overlap among native large terrestrial carnivores in south Florida.

Sorenson's similarity coefficient comparisons (based on species occurrence in diet)

Species	Bobcat	Florida panther	Black bear
Bobcat	1		
Florida panther	0.57	1	
Black bear	0.17	0.19	1

Pianka's resource overlap algorithm comparisons (based on percent occurrence in diet)

Species	Bobcat	Florida panther	Black bear
Bobcat	1		
Florida panther	0.13	1	
Black bear	0.002	0.015	1

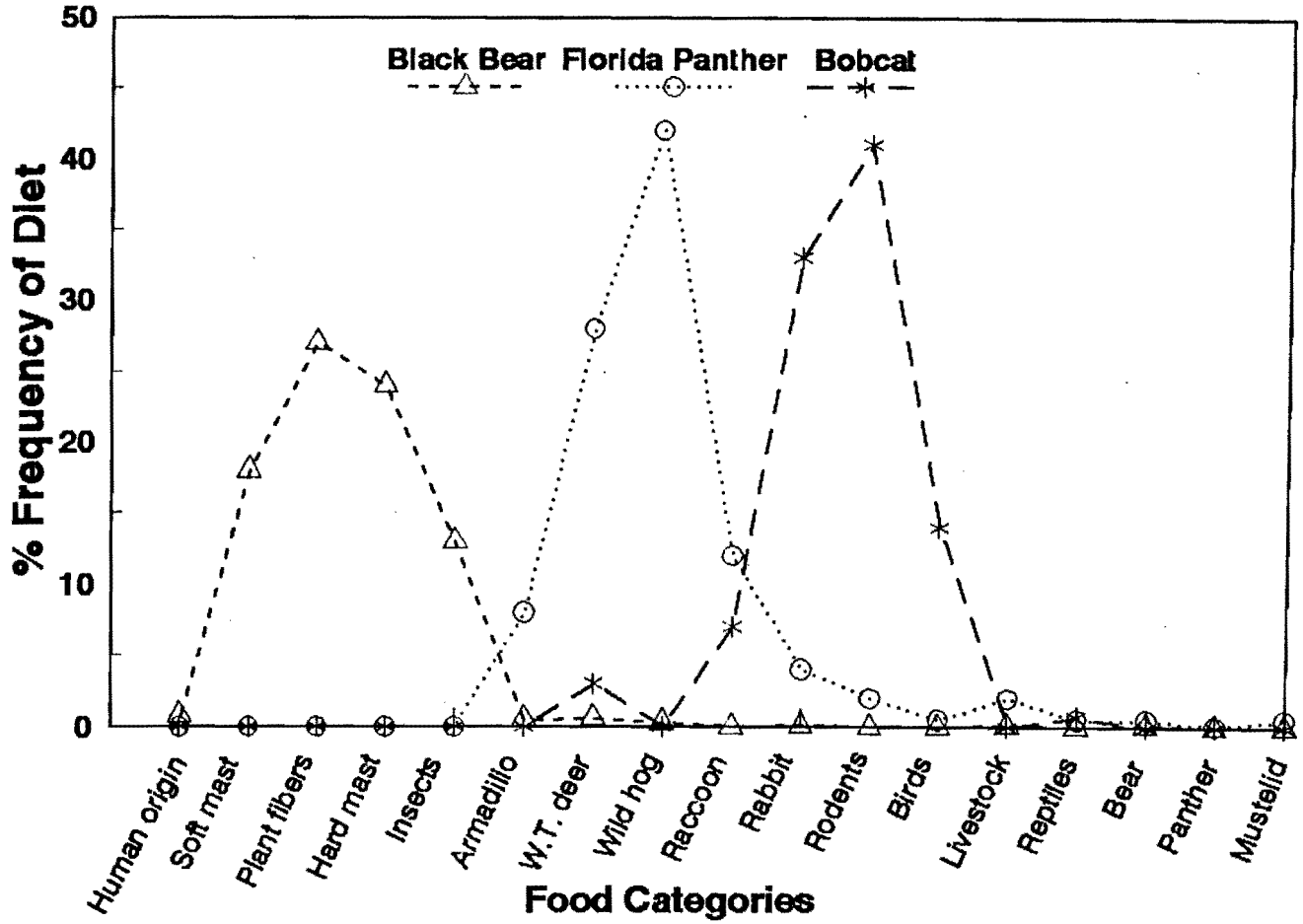


Figure 2.3. Food habits overlap among black bears, bobcats, and Florida panthers in southwest Florida.

1951, Westfall 1956, Beale and Smith 1973, Turkowski 1980, Toweill and Anthony 1988), south Florida provides conditions that do not compel these carnivores to consistently prey upon large vertebrates. Prevailing climatic conditions prolong growing seasons for temperate plant species, allow the establishment of both naturally and artificially established tropical plants, and encourage stability in prey populations. These factors may help to explain the infrequent predation by south Florida black bears on large vertebrate prey, infrequent killing of livestock by panthers, and the predominance in south Florida bobcat diets of small-sized prey throughout the year. Moreover, influxes of wintering migrant birds boosts prey opportunities without requiring bobcats to shift their home ranges in order to maintain nutrition during temporary periods of small mammal scarcity.

The black bear, Florida panther, and bobcat trace their ancestries well before the Pleistocene (Webb 1974) at a time when very different environmental conditions prevailed. Stirling and Derocher (1989) suggested that the black bear has remained virtually unchanged for $1x10^6$ years, and all three species have adapted to changes in food availability that can be measured over geological time. Florida's three native carnivores are similar inasmuch as they are all adaptable species that can fill distributional extremes. It is of interest that interference competition has been documented in the relatively open Everglades (where panthers killed and consumed bobcats, O.L. Bass pers. comm.), and bobcats were the major source of mortality to an open, freshwater-marsh-dwelling white-tailed deer population in Big Cypress National Preserve (Land et al. 1993). In the latter case, panthers were also permanent residents but avoided the open marshes where bobcats

preyed on deer. Hence, utilization of a similar food source was facilitated by habitat separation in the Big Cypress Swamp, but in the relatively treeless Everglades, panthers exerted interference competition over the bobcat. Despite the panther's competitive dominance, bobcats are now the only native cat species permanently inhabiting southeastern Florida. It is possible that the existing carnivore community in southeastern Florida, where the largest two species are now rare, is an artifact of human-induced landscape changes in the region. The elimination of the Atlantic Coastal Ridge forest that once bordered the herbaceous expanse known as the Everglades, may be the most significant factor in the decline of black bears and Florida panthers in southeastern Florida, and may explain the local abundance of bobcats. In general, however, available food appears to be effectively partitioned among the region's three largest carnivores where forests dominate the landscape.

CHAPTER 3

HABITAT USE AMONG SOUTH FLORIDA'S LARGE MAMMALIAN CARNIVORES

A diverse array of large mammalian herbivores in East Africa uses the same space by partitioning food resources (Lamprey 1963, Jarman and Sinclair 1979). In the same landscape, five large mammalian predators utilize a common herbivore biomass by a variety of social strategies, preying on different species, or even partitioning the same species (Bertram 1979). These are but two examples of resource partitioning among similar species and illustrate coexistence among organisms with similar life styles (see Caughley and Sinclair 1994:145). They provide evidence that the prospect of competition can result in intricate resource partitioning mechanisms.

Most of the aforementioned studies occurred in settings where food habits and habitat preferences could be determined by direct observation. In south Florida, terrestrial carnivore behavior is hidden beneath a canopy of dense forest and/or darkness, thus interpretations of habitat use are complicated by secretive species. Aerial radio-telemetry eliminates the problem of error implicit in ground triangulation, but flights restricted to daylight hours may uncover only a portion of these species' spatial activities (Mech 1983) and most behavior must be inferred from interpretation of spoor and telemetry data. Thus,

inferences made about habitat use must be viewed with caution, especially if the study species are nocturnal or crepuscular.

Maehr et al. (1991) found that nine Florida panthers monitored from 1985-1989 preferred upland forests over open and/or denatured habitats. However, this analysis ignored the potential impacts of annual variation and social status of the study animals. Habitat use analyses in Maehr et al. (1991) included two non-reproductive adult females (#08, #18), two non-resident adult males (#13, #20), and an adult female that was captured as a kitten (#19). Foster (1992) examined home range use patterns in south Florida bobcats but did not consider seasonal effects, nor habitat use relative to its availability. Wassmer et al. (1988) examined bobcat ecology in south-central Florida and found that among natural habitats closed-canopy forests were preferred over more open forests. Habitat preferences in south Florida black bears have not previously been examined.

Maehr and Cox (1995) utilized over 10 years of telemetry data to illustrate the importance of forest cover in explaining panther distribution and abundance throughout south Florida. At such a large scale, inherent biases in landscape data such as inaccurate cover type identification, are likely insignificant. But even at the scale of individual study animals, observations of field sign, and the trailing behavior of hounds have not revealed patterns of habitat use that differ from previous analyses of telemetry data (Maehr et al. 1990, 1991). Although I have seen tracks of panthers in unforested settings, their discovery in such open areas is unusual, and the appearance of these tracks usually indicates directional travel to the nearest forest patch. Black bears were found to be

active primarily during daylight in south Florida (see home range and land tenure chapter), and the discovery of bobcat sign is most often associated with trails through wooded terrain (pers. observ.) suggesting that bobcats do not venture far from forest cover. Therefore, even though this study is based upon daylight data collection, strong inference of overall applicability to habitat use patterns among panthers, black bears, and bobcats in south Florida seems reasonable. This chapter focuses on patterns of habitat use exhibited by south Florida's large mammalian carnivores as revealed by radio-telemetry.

Methods

Habitat use was determined by identifying the vegetative cover types associated with each radio location. While radio locations were fixed points defined as Universal Transverse Mercator (UTM) coordinates, error associated with observer variance, and map accuracy precluded the determination of habitat type solely from this cartographic system. Using the aerial tracking methodology described by Mech (1983), vegetative cover types were recorded as independent variables that were associated with a pair of UTM coordinates. Thus, even though some coordinate pairs may have imprecisely pinpointed a two-dimensional location, the habitat type was not affected by as many potential sources of error.

Annual variation in habitat use was examined by comparing years for those individuals that were monitored for greater than one year. Florida panthers are represented by several animals that were monitored for more than three years, whereas most black bears were monitored for fewer than three years. Bobcat transmitters rarely functioned for more than one year, so this species was not included in this analysis. Chi-

square analysis (P=0.05) was used to compare habitat percent frequencies between consecutive years for selected individuals that were monitored for more than one year.

Multiple analysis of variance (PROC MANOVA, SAS Institute, Inc. 1988) was used to determine whether habitat variables differentiated species and gender groups within each of 3 seasons (Winter=January-April, Summer=May-August, Fall=September-December). Wilks' Lambda scores ($P<0.05$) were used to indicate if the total model detected significant differences within seasons because meaningful patterns could exist even when no individual habitat types exhibited significant differences among species or gender groups. When differences were indicated by the overall analysis, significant differences among species, within individual habitat types, were determined. These frequency data were used in subsequent factor analyses to help clarify observed patterns of habitat overlap based on percent frequency occurrence. Factor analysis (SAS Institute, Inc. 1988) was performed for each sex-x-season combination (n=6) using habitat variables that were used regularly by all three species. Mean factor scores were then calculated and plotted for each sex-x-season combination for factors that accounted for at least the average amount of model variance.

Habitat use patterns were determined by comparing the percent frequency of habitat use of individual resident adult study animals with the composition of concave polygons that encompassed all resident home ranges of each species from 1986 through 1994 (Fig. 3.1). Concave polygons were determined using McPaal (Stuwe 1985), and were used in order to exclude areas that resident adults did not use. Thus, areas such as suburban Naples, FL were excluded from the habitat available to resident adults even

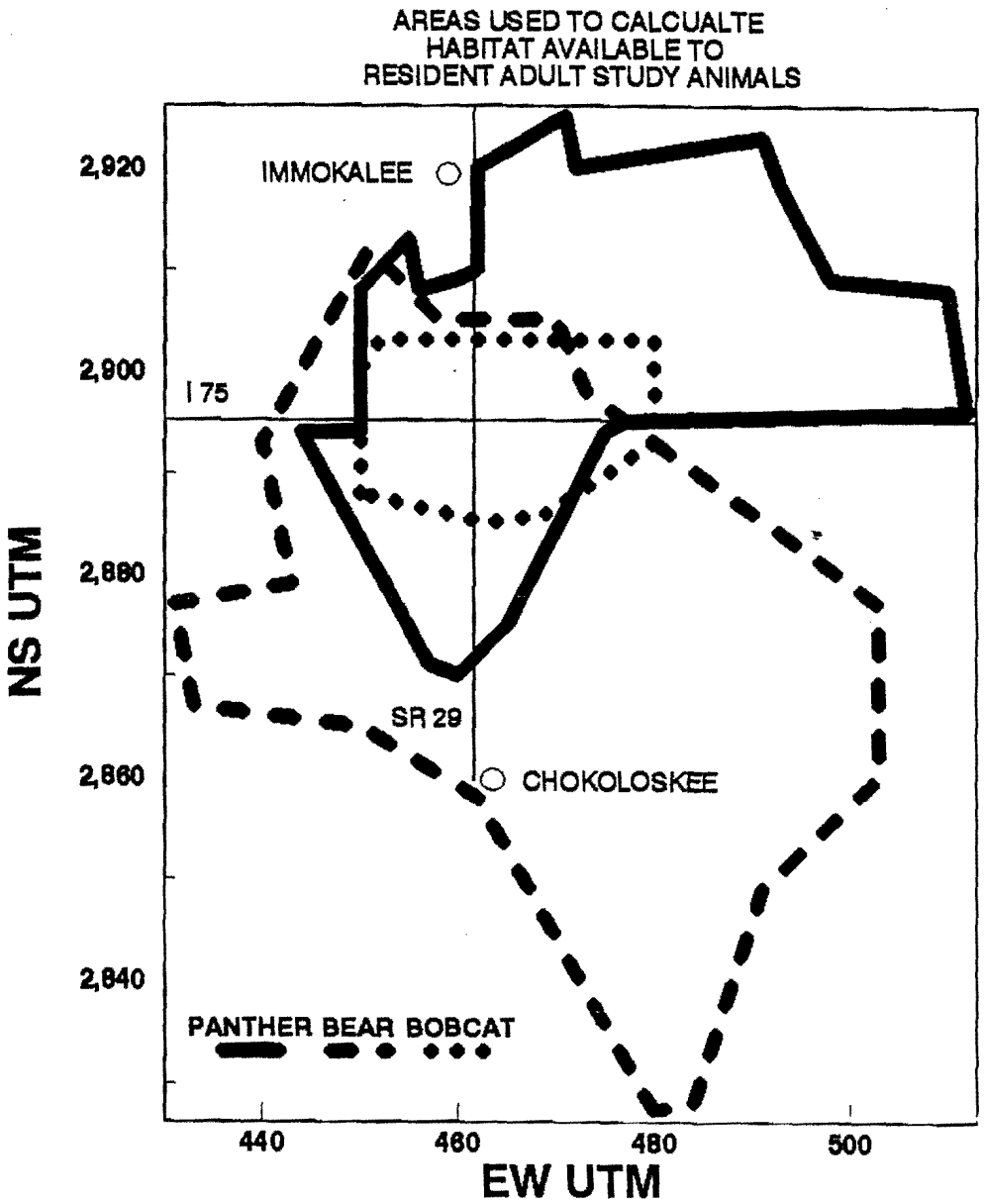


Figure 3.1. Concave polygons for black bear, bobcat, and Florida panther habitat analyses. Species polygons encompass all resident home ranges of adults studied from 1986 - 1994.

though dispersers of all three species were found in such peripheral range. Chi-square analysis (P=0.05) was used to compare the composition of concave polygons of a given species (expected habitat use exhibited by all individuals) with the composition of habitat types determined from radio telemetry for each individual within that species (observed habitat use). Although patterns of habitat selection and avoidance have previously been based on a comparison of used versus available habitat within individual home ranges(Maehr et al. 1991), this method presumes that the selection of a home range is independent of the spatial arrangement of conspecifics and distribution of landscape features that make up habitat for that particular species. As was observed among dispersing subadults of all three species, some individuals traveled widely within the permanently occupied range for that species and occasionally ventured into areas that were unsuitable for permanent occupation. Although individuals such as female panther #52 expanded the known breeding distribution for the species, most dispersal movements resulted in only temporary occupation outside of the core breeding area.

I examined seasonal home ranges of all adult bobcats (four males, four females), five adult male black bears, five adult female black bears, five adult female panthers, and five adult male panthers, and calculated habitat use patterns for each season. Individuals were selected in order to represent as much of the study area as possible. Subadults and dispersing individuals were disqualified from these analyses.

Habitat availability was determined by using 1985-1989 geo-referenced Landsat Thematic Mapper imagery (Kautz et al. 1993), and SPANS geographic information system software (TYDAC 1991). Although Kautz et al. (1993) recognized 22 land cover

types, not all of them were represented in south Florida, and several could not be consistently differentiated from others with similar reflective qualities. For example pine/cabbage palm forests were not distinguishable from pine flatwoods, cabbage palm woodlands were similar to hardwood hammocks, and grasslands and dry prairies were not distinguishable from each other. As a result, for chi-square analyses that required comparisons of used versus available habitat, I used nine cover types that were readily distinguishable from each other. This classification is similar to the one used by Maehr et al. (1991) for the Florida panther, with the principal difference being that it included mangroves as a separate category, and incorporated salt marsh into the herbaceous marsh category. The nine cover types recognized include: pine flatwoods (PP), hardwood hammock (HH), mixed swamp (MS), cypress swamp (CS), thicket swamp (TS), herbaceous marsh (MA), dry prairie (DP), agricultural/disturbed (AD), and mangroves (MG).

Habitat overlap between species was determined by comparing overlap coefficients based on percent frequencies of seasonal habitat use (Pianka 1986). Values approaching 1.0 represent maximum similarity in habitat use.

Results and Discussion

The sum total areas of radio-collared, permanent resident adults was 468 km^2 for bobcats, 2982 km^2 for black bears, and 1735 km^2 for Florida panthers (Fig. 3.1). The bobcat polygon was completely contained within the bear and panther polygons, however, black bear use of coastal areas created a zone of non-overlap with both cat species. As a

result, salt marshes and mangroves were available to black bears but not to bobcats and panthers.

Because the trapping of bobcats was opportunistic, and bobcats are known to range throughout south Florida, the polygon for this species certainly underrepresents occupied range. In other words, this area reflected only that portion of occupied range that encompassed resident study animals and included gaps between individuals that were likely used by uncollared bobcats. Because of their smaller home ranges and the variability inherent in the landscape, each bobcat sampled in this study was unlikely to experience the plant community diversity that was typical of the larger species. Thus, this sample is likely insufficient to reflect overall habitat use patterns for the species in south Florida. Black bears, on the other hand, were captured over a large area and this, coupled with their larger movements and larger sample sizes improved the reliability of generalizations about bear habitat-use patterns in south Florida. Similarly, the panther polygon represents extensive capture efforts and contains the core of permanently occupied range (Maehr et al. 1991, Maehr and Cox 1995). Thus, the estimates of panther and black bear habitat use probably represent use-patterns typical of their species than do the estimates for bobcats.

Florida panthers exhibited little variation in habitat use patterns between years (Table 3.1). Differences between consecutive years that were significant or that approached significance for individual panthers were usually related to social dynamics that influenced home range shape and size. For example, during 1987 and 1988 female panther #09 gradually shifted her home range to the more heavily forested Fakahatchee Strand as the result of the removal of female panther #08 and the home range vacancy that was created by this artificial abandonment in April 1987. Male panther #12 exhibited

Table 3.1. Annual habitat use comparisons for black bears and Florida panthers monitored for multiple years using Chi-square analysis (P=0.05). Probabilities in bold face represent significant differences between individual habitat use in one year versus the previous year.

		Habitat type[1]										
		PP	HH	MS	CS	TS	MA	DP	AD	MG		
ID#	Year				Female panthers						Chi[2]	P
09	1986	19.6	20.9	34.8	12.9	1.1	0	0.6	0	-	-	-
09	1987	12.0	38.7	40.8	7.7	0	0	0.7	0	-	10.0	0.07
09	1988	7.6	26.7	46.5	19.1	0	0	0	0	-	9.1	0.06
09	1989	3.7	16.1	52.8	26.7	0.6	0	0	0	-	6.2	0.18
09	1990	7.0	20.5	59.0	12.2	0.6	0.6	0	0	-	7.9	0.16
09	1991	11.5	26.6	52.5	8.6	0	0	0	0.7	-	4.7	0.57
09	1992	16.6	24.7	53.3	6.7	0	0.7	0	0	-	2.6	0.75
09	1993	12.2	23.0	56.1	8.8	0	0	0	0	-	1.8	0.77
09	1994	11.0	18.1	67.7	3.1	0	0	0	0	-	4.5	0.21
36	1990	30.7	24.3	7.1	37.9	0	0	0	0	-	-	-
36	1991	43.7	24.3	9.0	22.9	0	0	0	0	-	6.2	0.10
36	1992	54.7	22.0	10.7	12.7	0	0	0	0	-	4.4	0.22
36	1993	50.7	14.9	10.1	24.3	0	0	0	0	-	5.2	0.16
36	1994	47.6	25.8	14.5	12.1	0	0	0	0	-	7.9	0.05
					Male panthers							
12	1986	26.5	39.1	22.3	11.4	0.6	0	0	0	-	-	-
12	1987	32.1	22.6	29.8	14.9	0	0	0	0.6	-	7.7	0.17
12	1988	17.4	23.9	34.2	23.2	0.6	0.6	0	0	-	8.3	0.22
12	1989	19.9	27.7	16.3	30.1	5.4	0	0.6	0	-	12.7	0.05
12	1990	21.9	25.6	21.2	28.7	1.9	0	0	0.6	-	3.7	0.71
12	1991	28.7	40.7	14.7	15.3	0	0	0	0	-	12.1	0.03
12	1992	24.5	37.7	14.6	22.5	0.7	0	0	0	-	2.5	0.64
12	1993	32.4	42.7	13.8	10.3	0.7	0	0	0	-	5.9	0.20
12	1994	37.4	48.7	7.3	5.7	0.8	0	0	0	-	4.1	0.05
17	1987	32.9	36.2	14.1	14.1	0	0	2.7	0	-	-	-
17	1988	29.7	44.9	5.7	19.6	0	0	0	0	-	8.2	0.08
17	1989	28.4	45.8	7.1	16.8	1.3	0	0.6	0	-	2.3	0.80
					Female black bears							
F02	1992	50.6	25.9	7.4	12.3	1.2	1.2	0	1.2	0	-	-
F02	1993	22.4	30.2	21.0	18.4	1.3	0	0	6.6	0	23.9	0.0005
F02	1994	15.5	21.8	6.2	23.4	10.9	0	0	21.9	0	27.0	<0.0001
F03	1993	5.3	20.0	56.0	16.0	0	0	0	2.7	0	-	-
F03	1994	12.5	26.5	50.0	7.8	1.6	1.6	0	0	0	12.9	0.04
F09	1992	12.2	19.5	2.4	8.5	3.7	3.7	0	3.7	46.3	-	-
F09	1993	16.9	19.7	4.2	7.0	4.2	2.8	0	1.4	43.7	2.7	0.91
F19	1993	26.7	32.0	24.0	8.0	6.7	2.7	0	0	0	-	-
F19	1994	21.2	30.3	43.9	3.0	0	1.5	0	0	0	8.8	0.26

Table 3.1. (continued)

		Habitat type[1]										
		PP	HH	MS	CS	TS	MA	DP	AD	MG		
		Male black bears										
M02	1991	7.3	35.3	4.4	2.9	8.8	8.8	0	0	32.3	-	-
M02	1992	6.3	30.4	8.9	1.3	6.3	15.2	0	3.8	27.8	8.8	0.26
M08	1992	24.7	9.1	14.3	46.7	2.6	1.3	0	1.3	0	-	-
M08	1993	25.9	6.5	9.1	46.7	0	1.3	0	10.4	0	11.3	0.08
M13	1992	33.7	15.0	3.7	18.7	0	0	0	27.5	1.2	-	-
M13	1993	39.7	9.6	8.2	12.3	9.6	1.4	0	6.8	12.3	37.3	**<0.0001**
M13	1994	35.2	25.9	13.0	9.3	1.8	1.8	0	13.0	0	28.9	**<0.0001**
M18	1992	42.6	8.8	22.1	11.8	2.9	1.5	1.5	5.9	2.9	-	-
M18	1993	47.7	8.9	14.9	9.0	7.5	1.5	1.5	9.0	0	7.6	0.47

[1]PP=pine/palmetto, HH=hardwood hammock, MS=mixed swamp, CS=cypress swamp, TS=thicket swamp, MA=freshwater and salt marsh, DP=dry prairie, AD=agricultural/disturbed, MG=mangroves.

several habitat-use shifts that were related to the colonizations and deaths of resident males in adjoining home ranges during 1989 and 1991 (Table 3.1)(see home range and land tenure chapter). This interpretation is supported by the observation that panther #12's use of mixed swamp declined in those years following a withdrawal from the Fakahatchee Strand, a system dominated by this forested wetland. Number 12's final habitat-use shift that preceded his death in 1994 was apparently related to failing health and a shrinking home range. While it is possible that differences in panther habitat use may also be influenced by annually fluctuating food supplies, previous studies suggest that deer populations have remained stable in space and time in south Florida (Land et al. 1993) and are thus unlikely to influence panther habitat use.

Female black bears exhibited the greatest variability between years. These differences were probably related to reproduction and denning when females spend several months in a restricted area and small cubs restrict their movements. Although mast supplies were not measured in this study, qualitative comparisons suggest that concentrations of important foods such as saw palmetto fruit and acorns changed in spatial distribution annually. Such varying nutritional opportunities and subsequent movements to access alternative food supplies may explain the variation in habitat use demonstrated by male black bear M13 (Table 3.1).

Significant differences (P=0.001) in seasonal habitat use patterns were observed among all species/gender groups for several habitat variables (Tables 3.2 and 3.3). Females tended to differ on more habitat dimensions than males (Table 3.2). Habitats that were used differently by females in all seasons included hardwood hammock, mixed

Table 3.2. Habitat use differences among female bobcats, black bears and panthers in south Florida as determined by multiple analysis of variance (P=0.05) of habitat use frequencies. Only those habitats that indicated significant differences are reported.

	Winter	
Wilks' Lambda=0.0594	F=6.2	P=0.0001
Habitat type	F	P
Hardwood hammock	12.44	0.0001
Cabbage palm	5.17	0.0113
Mixed swamp	4.05	0.027
Cypress swamp	6.40	0.0046
Herbaceous marsh	3.79	0.0333
Mangrove	3.35	0.048
	Summer	
Wilks' Lambda=0.0556	F=5.67	P=0.0001
Habitat type	F	P
Pine flatwoods	3.47	0.0433
Pine/cabbage palm	4.17	0.0247
Hardwood hammock	16.97	0.0001
Mixed swamp	3.65	0.0374
Cypress swamp	5.40	0.0095
Dry prairie/grassland	6.57	0.0041
	Fall	
Wilks' Lambda=0.0585	F=6.00	P=0.0001
Habitat type	F	P
Pine/cabbage palm	13.35	0.0001
Hardwood hammock	7.35	0.0022
Cabbage palm	5.78	0.0069
Mixed swamp	6.82	0.0032
Cypress swamp	6.26	0.0049

Table 3.3. Habitat use differences among male bobcats, black bears and panthers in south Florida as determined by multiple analysis of variance (P=0.05) of habitat use frequencies. Only those habitats that indicated significant differences are reported.

	Winter	
Wilks' Lambda=0.1064	F=3.443	P=0.0003
Habitat type	F	P
Pine flatwoods	5.14	0.0118
Hardwood hammock	17.00	0.0001
Mixed swamp	6.34	0.0049
Agricultural/disturbed	5.29	0.0106
	Summer	
Wilks' Lambda=0.012	F=9.665	P=0.0001
Habitat type	F	P
Pine flatwoods	4.15	0.0279
Pine/cabbage palm	3.77	0.0370
Hardwood hammock	11.74	0.0003
Agricultural/disturbed	3.61	0.0421
	Fall	
Wilks' Lambda=0.143	F=2.684	P=0.0041
Habitat type	F	P
Pine/cabbage palm	4.36	0.0225
Hardwood hammock	11.67	0.0002
Mixed swamp	3.50	0.0440
Agricultural/disturbed	5.29	0.0113

swamp, and cypress swamp. Habitats that were used differently by males in all seasons were hardwood hammock and agricultural/disturbed (Table 3.3). It is likely that female habitat use was influenced by the confounding combination of smaller bear and panther home ranges and the effects of pregnancy, denning, and dependent young on all three species. Localized movements due to dependent cubs and kittens undoubtedly increased the use of areas near preferred den sites and reduced the use of more distant preferred habitat that would otherwise have been used had these females been solitary.

Percent frequency of habitat use based on individual analyses indicate that forest cover is used by panthers (Table 3.4), black bears (Table 3.5), and bobcats (Table 3.6) nearly to the exclusion of maritime and unforested cover types (Fig. 3.2). Further, in every season, south Florida's large carnivores used land cover types in different proportions than they were available ($P<0.05$)(Table 3.7). This was due primarily to an avoidance by most individuals of herbaceous or otherwise unforested habitats. For example, herbaceous marshes covered from 12.8% to 24.0% of each habitat availability polygon, yet 3.2% was the most this cover type was used (Table 3.8). Pine flatwoods (including pine/cabbage palm) were universally preferred by all three species in every season. Bears used hardwood hammock slightly more than it was available, whereas male bobcats exhibited a marginal aversion to this cover type. The latter finding, however, may be a consequence of the small bobcat sample size inasmuch as male bobcat M02 used hardwood hammock in proportions that were more than twice its availability (Table 3.6).

Cypress swamps appeared to be used less than available by all species, while mixed swamp, a more thickly vegetated plant community, was used in varying proportions by study animals. Bobcats appeared to avoid mixed swamp communities, but this cover type

Table 3.4. Seasonal habitat use by Florida panthers, 1986-1994. Abbreviations are: PP=pine flatwoods, HH=hardwood hammock, MS=mixed swamp, CS=cypress swamp, TS=thicket swamp, MA=freshwater and saltwater marsh, DP=dry prairie and grassland, AD=agricultural/disturbed, and MG=mangroves.

				Florida panther habitat use (percent frequency)								
ID#	Sex	Season	Year	PP	HH	MS	CS	TS	MA	DP	AD	MG[1]
09	F	W	1986	14	29	34	21	2	0	0	0	-
11	F	W	1986	30	5	8	8	0	0	0	0	-
19	F	W	1992	39	24	16	18	0	0	0	2	-
31	F	W	1993	51	31	4	10	2	0	0	2	-
32	F	W	1992	20	20	33	26	0	0	0	0	-
09	F	S	1986	17	25	51	5	2	0	0	0	-
11	F	S	1986	31	54	9	3	2	0	0	0	-
19	F	S	1992	22	26	16	36	0	0	0	0	-
31	F	S	1993	27	19	10	37	4	2	0	0	-
32	F	S	1992	44	19	17	19	0	0	0	0	-
09	F	F	1986	28	39	18	12	0	0	2	0	-
11	F	F	1986	30	32	17	20	0	0	0	0	-
19	F	F	1992	40	34	14	12	0	0	0	0	-
31	F	F	1993	42	18	16	14	6	0	0	4	-
32	F	F	1992	37	37	10	14	0	0	0	2	-
12	M	W	1986	22	38	27	13	0	0	0	0	-
13	M	W	1987	27	46	15	3	5	0	2	0	-
26	M	W	1993	53	28	6	12	0	0	0	0	-
46	M	W	1993	23	58	4	12	2	0	0	0	-
51	M	W	1994	31	13	36	14	0	0	0	0	-
12	M	S	1986	19	51	21	9	0	0	0	0	-
13	M	S	1987	26	41	13	9	0	4	6	0	-
26	M	S	1993	47	36	6	13	0	0	0	0	-
46	M	S	1993	23	47	6	21	2	0	0	0	-
51	M	S	1994	22	18	53	6	0	0	0	0	-
12	M	F	1986	39	28	18	13	2	0	0	0	-
13	M	F	1987	42	37	4	16	0	0	0	0	-
26	M	F	1993	51	33	8	8	0	0	0	0	-
46	M	F	1993	27	57	2	12	0	2	0	0	-
51	M	F	1994	43	43	14	0	0	0	0	0	-

[1]This cover type was not available to adult resident individuals in the study area.

Table 3.5. Seasonal habitat use by south Florida black bears, 1991-1993. Abbreviations are: PP=pine flatwoods, HH=hardwood hammock, MS=mixed swamp, CS=cypress swamp, TS=thicket swamp, MA=freshwater and saltwater marsh, DP=dry prairie and grassland, AD=agricultural/disturbed, and MG=mangroves.

				Florida panther habitat use (percent frequency)								
ID#	Sex	Season	Year	PP	HH	MS	CS	TS	MA	DP	AD	MG
F02	F	W	1992	73	23	0	0	3	0	0	0	0
F03	F	W	1993	0	0	83	17	0	0	0	0	0
F04	F	W	1992	3	26	42	22	6	0	0	0	0
F05	F	W	1992	0	12	4	0	4	0	0	4	75
F06	F	W	1992	55	34	0	3	0	0	0	7	0
F02	F	S	1992	23	15	31	8	11	11	0	0	0
F03	F	S	1993	4	8	67	12	0	0	0	8	0
F04	F	S	1992	8	32	40	20	0	0	0	0	0
F05	F	S	1992	0	8	0	0	0	4	0	4	75
F06	F	S	1992	41	30	7	22	0	0	0	0	0
F02	F	F	1992	36	16	12	28	0	4	0	4	0
F03	F	F	1993	11	48	22	18	0	0	0	0	0
F04	F	F	1992	42	12	33	12	0	0	0	0	0
F05	F	F	1992	15	15	4	4	0	0	0	15	46
F06	F	F	1992	69	11	8	11	0	0	0	0	0
M06	M	W	1991	36	27	18	9	0	0	0	9	0
M08	M	W	1992	7	3	17	62	7	0	0	1	0
M13	M	W	1993	25	0	0	4	29	4	0	12	25
M18	M	W	1992	16	16	21	10	5	0	0	21	10
M20	M	W	1993	74	13	4	9	0	0	0	0	0
M06	M	S	1992	7	36	36	0	0	0	0	21	0
M08	M	S	1992	25	12	17	46	0	0	0	0	0
M13	M	S	1993	26	17	22	26	0	0	0	0	9
M18	M	S	1992	23	4	38	23	4	4	4	0	0
M20	M	S	1993	32	23	9	32	4	0	0	0	0
M06	M	F	1992	26	13	43	13	0	4	0	0	0
M08	M	F	1992	50	14	9	32	0	4	0	0	0
M13	M	F	1993	65	11	4	8	0	0	0	8	4
M18	M	F	1992	87	9	4	0	0	0	0	0	0
M20	M	F	1993	40	40	4	4	4	8	0	0	0

Table 3.6. Seasonal habitat use by south Florida bobcats, 1986-1987. Abbreviations are: PP=pine flatwoods, HH=hardwood hammock, MS=mixed swamp, CS=cypress swamp, TS=thicket swamp, MA=freshwater and saltwater marsh, DP=dry prairie and grassland, AD=agricultural/disturbed, and MG=mangroves.

				Bobcat habitat use (percent frequency)								
ID#	Sex	Season	Year	PP	HH	MS	CS	TS	MA	DP	AD	MG[1]
F03	F	W	1986	64	0	0	28	0	7	0	0	-
F06	F	W	1987	64	36	0	0	0	0	0	0	-
F07	F	W	1987	64	14	0	21	0	0	0	0	-
F03	F	S	1986	72	11	3	14	0	0	0	0	-
F06	F	S	1987	23	61	0	8	0	0	8	0	-
F07	F	S	1987	65	12	0	18	0	0	6	0	-
F09	F	S	1987	40	60	0	0	0	0	0	0	-
F03	F	F	1986	83	14	0	3	0	0	0	0	-
F06	F	F	1987	40	20	0	0	0	0	40	0	-
F07	F	F	1987	22	0	0	44	0	0	22	11	-
M01	M	W	1986	88	6	0	6	0	0	0	0	-
M02	M	W	1986	45	45	4	4	0	0	0	0	-
M05	M	W	1987	77	0	0	9	4	0	0	9	
M08	M	W	1987	36	0	18	18	0	0	0	27	-
M01	M	S	1986	76	10	0	13	0	0	0	0	-
M02	M	S	1986	67	16	2	8	4	2	0	0	-
M08	M	S	1987	0	7	28	14	0	0	0	50	-
M01	M	F	1986	87	3	0	0	0	0	10	0	-
M02	M	F	1986	46	54	0	0	0	0	0	0	-
M05	M	F	1986	68	11	0	14	0	0	0	6	-
M08	M	F	1987	28	0	0	28	0	0	43	0	-

[1]This cover type was not available to adult resident individuals in the study area.

Table 3.7. Chi-square values and probabilities for seasonal comparisons between habitat available to and habitat used by large carnivores in south Florida, 1986-1994.

			Winter		Summer		Fall	
Species	Sex	ID#	Chi^2	*P*	Chi^2	*P*	Chi^2	*P*
Panther	F	09	57.6	<0.001	88.0	<0.001	62.0	<0.001
Panther	F	11	59.9	<0.001	92.0	<0.001	56.6	<0.001
Panther	F	19	54.5	<0.001	45.3	<0.001	70.1	<0.001
Panther	F	31	75.1	<0.001	38.6	<0.001	57.4	<0.001
Panther	F	32	53.3	<0.001	60.6	<0.001	62.5	<0.001
Panther	M	12	67.7	<0.001	77.3	<0.001	65.4	<0.001
Panther	M	13	81.5	<0.001	49.9	<0.001	71.0	<0.001
Panther	M	26	76.4	<0.001	75.7	<0.001	82.6	<0.001
Panther	M	46	77.6	<0.001	60.4	<0.001	77.5	<0.001
Panther	M	51	66.8	<0.001	87.8	<0.001	12.6	0.013
Bear	F	F02	140.5	<0.001	77.3	<0.001	59.8	<0.001
Bear	F	F03	128.5	<0.001	49.9	<0.001	77.9	<0.001
Bear	F	F04	77.8	<0.001	75.7	<0.001	97.5	<0.001
Bear	F	F05	106.5	<0.001	60.4	<0.001	82.5	<0.001
Bear	F	F06	126.8	<0.001	87.8	<0.001	106.4	<0.001
Bear	M	M06	95.1	<0.001	71.4	<0.001	81.2	<0.001
Bear	M	M08	65.8	<0.001	106.7	<0.001	69.6	<0.001
Bear	M	M13	106.2	<0.001	78.7	<0.001	103.5	<0.001
Bear	M	M18	72.9	<0.001	102.5	<0.001	145.8	<0.001
Bear	M	M20	113.9	<0.001	79.0	<0.001	89.2	<0.001
Bobcat	F	F03	90.4	<0.001	95.5	<0.001	128.2	<0.001
Bobcat	F	F06	121.0	<0.001	81.6	<0.001	123.8	<0.001
Bobcat	F	F07	87.7	<0.001	90.0	<0.001	89.1	<0.001
Bobcat	F	F09	-	-	113.4	<0.001	-	-
Bobcat	M	M01	133.5	<0.001	107.6	<0.001	153.4	<0.001
Bobcat	M	M02	89.7	<0.001	92.2	<0.001	114.7	<0.001
Bobcat	M	M05	137.2	<0.001	-	-	102.1	<0.001
Bobcat	M	M08	97.0	<0.001	53.1	<0.001	104.2	<0.001

Table 3.8. Comparison between habitat available and mean habitat use for south Florida carnivores, 1986-1994.

Sex/species		Habitat type								
Female panthers	Season	PP	HH	MS	CS	TS	MA	DP	AD	MG[1]
Available	-	**11.8**	**12.6**	**8.9**	**31.3**	**1.1**	**12.8**	**13.5**	**7.8**	-
Used	Winter	30.8	31.6	19.0	16.6	0.8	0	0	0.8	-
Used	Summer	28.2	28.6	20.6	20.0	1.6	0.4	0	0	-
Used	Fall	35.4	32.0	15.0	14.4	1.2	0	0.4	1.2	
Male panthers										
Available	-	**11.8**	**12.6**	**8.9**	**31.3**	**1.1**	**12.8**	**13.5**	**7.8**	-
Used	Winter	31.2	36.6	17.6	10.8	1.4	0	0.4	0	-
Used	Summer	27.4	38.6	19.8	11.6	0.4	0.8	1.2	0	-
Used	Fall	40.4	39.6	9.2	7.8	0.4	0.4	0	0	-
Female bears										
Available	-	**4.8**	**11.9**	**5.9**	**30.3**	**1.1**	**24.0**	**1.3**	**0.7**	**14.1**
Used	Winter	26.2	19.0	25.8	8.4	2.6	0	0	2.2	15.0
Used	Summer	15.2	18.6	29.0	12.4	2.2	3.0	0	2.4	15.0
Used	Fall	34.6	20.4	15.8	14.6	0	0.8	0	3.8	9.2
Male bears										
Available	-	**4.8**	**11.9**	**5.9**	**30.3**	**1.1**	**24.0**	**1.3**	**0.7**	**14.1**
Used	Winter	31.6	11.8	12.0	18.8	8.2	0.8	0	8.6	7.0
Used	Summer	22.6	18.4	24.0	25.4	1.6	0.8	0.8	4.2	1.8
Used	Fall	53.6	17.4	12.8	11.4	0.8	3.2	0	1.6	0.8
Female bobcats										
Available	-	**6.5**	**20.3**	**11.4**	**32.4**	**0**	**22.6**	**2.7**	**0.5**	-
Used	Winter	64.0	25.0	0	24.5	0	3.5	0	0	-
Used	Summer	50.0	36.0	0.6	10.0	0	0	3.5	0	-
Used	Fall	48.3	11.3	0	15.7	0	0	20.7	3.7	-
Male bobcats										
Available	-	**6.5**	**20.3**	**11.4**	**32.4**	**0**	**22.6**	**2.7**	**0.5**	-
Used	Winter	61.5	12.7	5.5	9.2	1.0	0	0	9.0	-
Used	Summer	47.7	11.0	10.0	11.7	1.3	0.7	0	16.7	-
Used	Fall	57.2	17.0	0	10.5	0	0	13.2	1.5	-

[1]This habitat type was not available to bobcats or panthers.

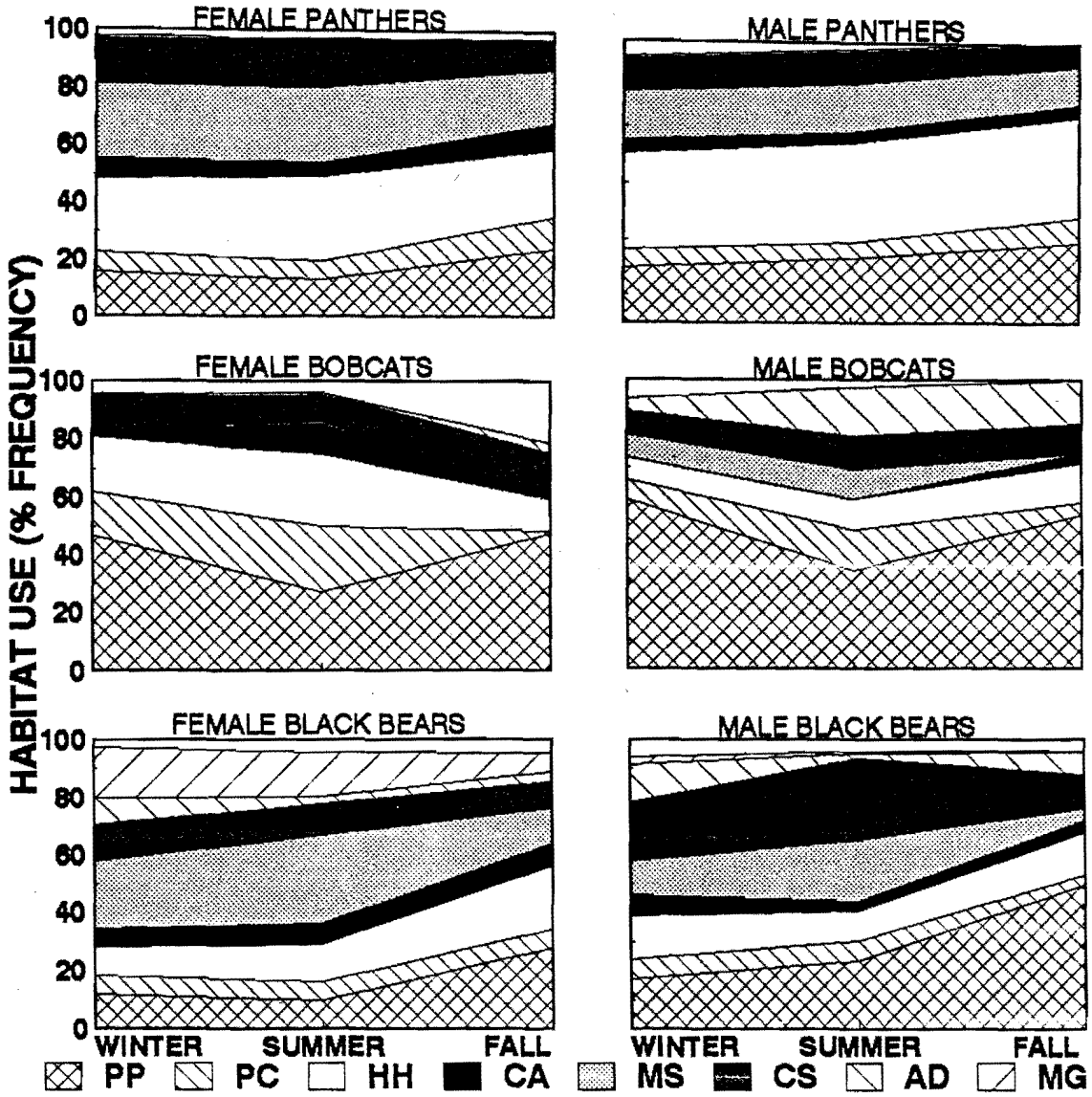


Figure 3.2. Seasonal habitat-use trends for female and male black bears, bobcats, and Florida panthers in south Florida, 1986 - 1994. PP= pine flatwoods, PC= pine cabbage palm, HH= hardwood hammock, CA= cabbage palm, MS= mixed swamp, CS= cypress swamp, AD= agricultural/disturbed, MG= mangrove swamp.

was not abundant in the bobcat habitat availability polygon. Most mixed swamp in Florida is found in the Fakahatchee Strand, where panthers have been known to reside since field searches were first conducted (Nowak and McBride 1973). This cover type was used slightly more than it was available to panthers, even though nutrition may be a problem for some individuals that reside there (Maehr et al. 1989). Black bears, especially females which were known to establish dens in this cover type, also used mixed swamp in a higher proportion than it occurred in the environment. Further, important black bear foods such as Thalia geniculata, and early mast-producing shrubs such as swamp dogwood (Cornus foemina) were abundant in the Fakahatchee Strand.

Two components common to the six habitats used regularly by all three species explained more than an average amount of variation in habitat use during each season (Table 3.9) (Fig. 3.3). Among these habitats, pine flatwoods accounted for the least variation suggesting that it was used consistently by all of south Florida's large carnivores (Table 3.10). The greatest variability during summer, however, was related to differential use of pine flatwoods and hardwood hammocks. Hammocks tended to be used more by female bobcats during summer than during other seasons, and by male panthers during every season. The disproportionately high use of this habitat by male panthers and female bobcats may explain the consistent divergence between male and female panthers throughout the year, and between male and female bobcats during summer. The conclusion of apparent differences between bobcat gender should be tempered because of small sample size. On the other hand, similar trends in male panther preferences for hardwood hammock were noted by Maehr and Cox (1995), and may represent resource partitioning that reduces the potential for competition between male and female panthers.

Table 3.9. Eigenvalues and proportions of variability explained by each of 5 factors that examine habitat use patterns in bobcats, black bears, and Florida panthers in southwest Florida.

	Factor				
Winter	I	II	III	IV	V
Eigenvalue	1.6752	1.5173	0.992	0.7164	0.5978
Proportion	0.28	0.25	0.16	0.12	0.10
Summer					
Eigenvalue	1.9756	1.2576	0.9351	0.823	0.6394
Proportion	0.33	0.21	0.15	0.14	0.11
Fall					
Eigenvalue	1.9572	1.4794	0.9155	0.6399	0.562
Proportion	0.33	0.25	0.15	0.11	0.09

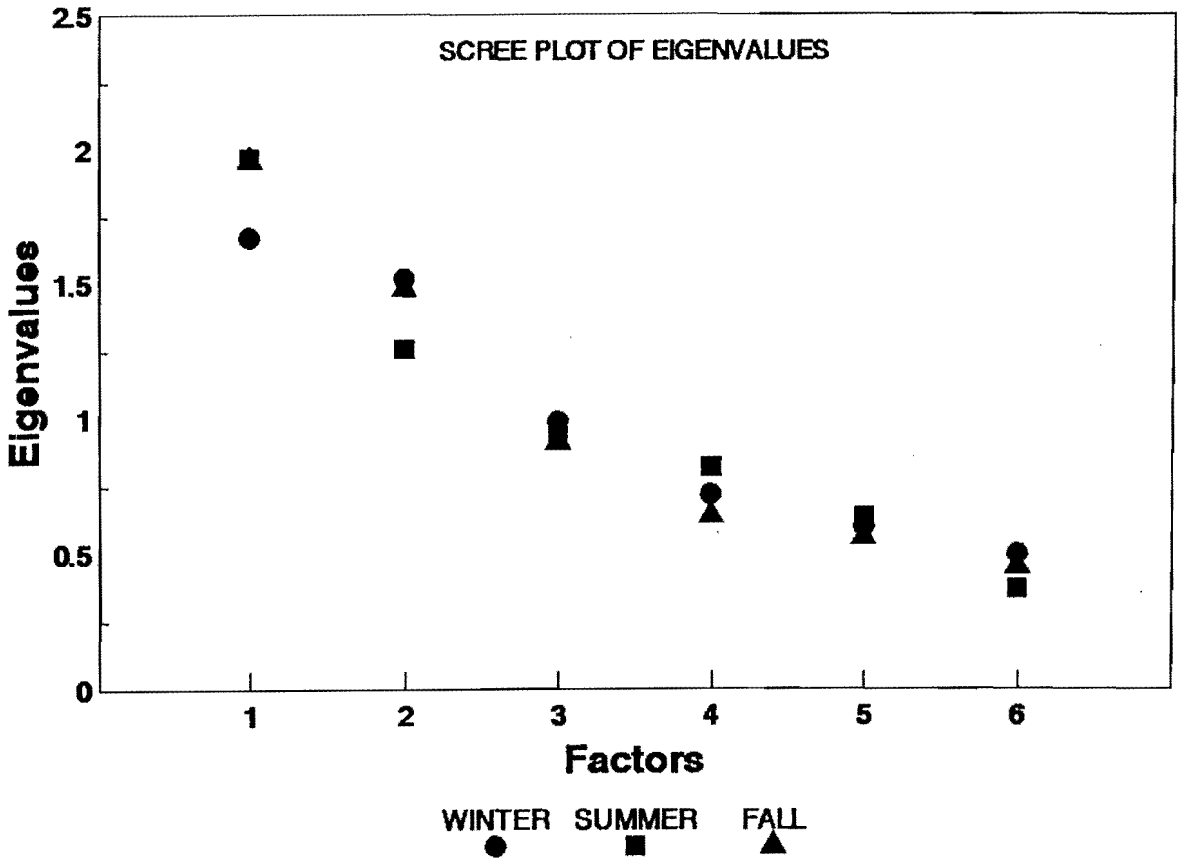


Figure 3.3. Scree plot of Eigenvalues used to select factors that explained at least an average amount of variation in habitat use of large mammalian carnivores in south Florida.

Table 3.10. Pearson correlation coefficients for habitat variables used by large mammalian carnivores in southwest Florida. Underlined values are significantly correlated with the observed variability in habitat use among bobcats, black bears, and Florida panthers. Values in parentheses are the probability that the habitat variable is not correlated with the observed variability.

	Habitat type					
	Pine flatwoods	Cabbage palm/pine	Hardwood hammock	Cabbage palm	Mixed swamp	Cypress swamp
			Winter			
Factor I	0.49732	**0.95275**	**0.96874**	**0.87926**	**0.93048**	**0.89386**
	(0.3155)	**(0.0033)**	**(0.0015)**	**(0.0210)**	**(0.0071)**	**(0.0163)**
Factor II	-0.49273	0.35626	0.28344	**0.82741**	0.70942	0.76051
	(0.3207)	(0.4882)	(0.5862)	**(0.0421)**	(0.1144)	(0.0792)
			Summer			
Factor I	**0.98865**	**0.87446**	0.27489	-0.44129	-0.26426	0.05092
	(0.0002)	**(0.0227)**	(0.5981)	(0.3810)	(0.6128)	(0.9237)
Factor II	0.25913	0.18144	**0.89598**	0.61557	0.70703	0.57216
	(0.620)	(0.7308)	**(0.0157)**	(0.1933)	(0.1162)	(0.2354)
			Fall			
Factor I	-0.05268	**0.97957**	**0.86621**	**0.90044**	**0.99509**	**0.96325**
	(0.921)	**(0.0006)**	**(0.026)**	**(0.0144)**	**(0.0001)**	**(0.002)**
Factor II	0.59210	0.70811	**0.85509**	0.26351	0.57605	0.70681
	(0.2156)	(0.1154)	**(0.030)**	(0.6139)	(0.2315)	(0.1163)

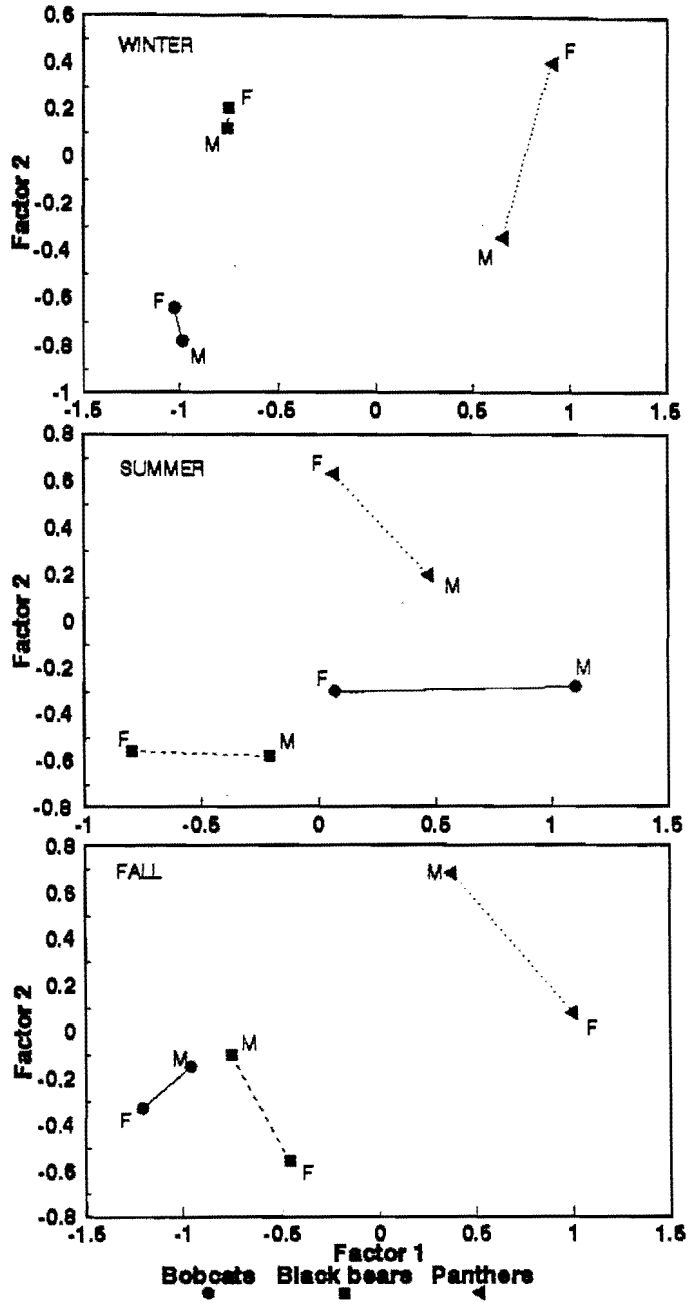


Figure 3.4. Factor analysis of habitat use patterns among female and male bobcats, black bears, and Florida panthers in south Florida.

The panther was the only species that exhibited consistent divergence in seasonal habitat-use across seasons (Fig. 3.4). Although food-habits studies have not demonstrated differences related to gender (Maehr et al. 1990), Harlow (1959) found that hardwood hammocks were the most productive habitats for white-tailed deer, and sign of wild hogs is more frequently encountered in this habitat type than elsewhere (pers. observ.). If male panthers use hardwood hammocks disproportionately because larger prey are more available in this upland plant community, then this may represent the causal mechanism that facilitates niche separation between male and female panthers. Such a pattern was not consistently found in the other two species.

Overall, considerable habitat overlap among species was apparent, but male and female panthers exhibited more niche separation than bears or bobcats, and panthers differed more by gender within species during summer than between species. When compared to panthers, bobcats and black bears exhibited more within-species similarity, suggesting that gender had less influence on habitat use-patterns for these species. If seasonal habitat shifts were made, both sexes experienced them. In general, panthers used pine flatwoods and hardwood hammocks more than expected from proportion in the landscape, whereas cypress swamp, thicket swamp, freshwater marsh, grasslands, and agricultural areas were used less than expected from simple availability (Table 3.8). These finding also support the conclusions of Maehr et al. (1991) that all panthers prefer upland forests. A reduction in bear use of mixed swamp and an increase in the use of pine flatwoods during fall was probably related to the wide-ranging excursions that many bears undertook to access abundant supplies of saw palmetto fruit. Black bears also used

agricultural/disturbed areas more than expected from mere abundance in the landscape. This likely was due to the abundance of Brazilian pepper thickets that often are associated with disturbed sites and agricultural edges. Brazilian pepper thickets frequently replace agricultural fields when they are abandoned, and this species is a common colonizer of roadsides, ditchbanks, and spoil (Loope and Dunevitz 1981, Ewel et al. 1982, Abrahamson and Hartnett 1990).

Black bears were the only species observed to utilize mangrove forests. Although use of maritime habitats by bears occurred year-round, the only activity that could be confirmed in these coastal swamps was denning by adult females. Male bears used mangroves proportionally less than their availability while females used this cover type proportional to availability. Perhaps mangroves are more important for cover than for the procurement of food, although black bears likely obtained some foods in mangroves. Foods that might draw non-denning black bears to mangroves are unknown. The densely branched growth form of mangroves, often dense swarms of mosquitoes, and deep organic soils make these areas nearly impenetrable to humans and other south Florida cursorial mammals. Extensive impenetrable areas made up of Rhododendron spp. and Smilax spp. are typical of much of inhabited black bear range (Pelton 1982:507). Despite the avoidance of unforested habitats by black bears, herbaceous wetlands adjacent to large mixed swamps and mangrove forests were occasionally used to obtain nutritious foods such as the nest-building colonial ant, Crematogaster pilosa (see dietary overlap chapter). An avoidance of mangroves by panthers was also observed by Smith and Bass (1994) in

Everglades National Park; an area where forested cover is sparse relative to forb- and sedge-dominated communities.

Even though Foster (1992) observed that the bobcats in her study sample were frequently found in mixed swamp, the sample in either study may not have been representative of the population. However, both studies were similar in demonstrating individual preferences for pine flatwoods that exceeded 60% (Foster 1992:72)(Table 3.6). Thicket swamps and freshwater marshes were used less than expected by bobcats in this study, while grasslands and agricultural/disturbed habitats were used to varying degrees in inconsistent seasonal patterns that may reflect individual variation among bobcats or small sample size.

Saw palmetto thickets appear to be universally important to bobcats in south Florida. Foster (1992) suggested that this common pine flatwoods understory plant was preferred, and Wassmer et al. (1988) found that saw palmetto thickets were important as natal dens. Female bobcat F03 denned in a palmetto thicket in the Bear Island Unit of the Big Cypress National Preserve during 1987, as did a female in Foster's (1992) study. Although Foster (1992) found that bobcats avoided agricultural areas, I found that male bobcats exhibited seasonally variable use of this cover type that exceeded its availability (Table 3.6). Wassmer et al. (1988) found that male bobcats used several agricultural cover types more frequently than expected even though citrus groves were avoided.

Capture locations of resident adult bobcats can no doubt bias subsequent interpretations of habitat use. Most of the animals studied by Foster (1992) were captured within the centers of large tracts of public lands, whereas several of the animals in this

study originated from private lands that bordered or included agricultural fields. Panthers and black bears were captured at widely scattered sites and they were found to move long distances compared to the relatively sedentary bobcats with smaller home ranges. Thus, by virtue of their smaller spatial requirements, bobcats captured on public lands were less likely to utilize agricultural habitats on adjacent private land. Unlike black bears and panthers, bobcats in this study did not demonstrate a consistent preference for hardwood hammocks; in fact, this cover type was used in lower proportions than its availability during all seasons by males and during fall by females. It is possible that the generally more open understory of hammocks may not provide the cover conditions that are typically found in saw palmetto thickets in pine flatwoods. The more solid canopy associated with live oak and cabbage palm hammocks creates shaded conditions at ground level that tend to reduce saw palmetto density. Snyder et al. (1990) did not list saw palmetto as a common understory species in south Florida hammocks, although it is found in every variation of this plant community. In addition, Loope and Urban (1980) found that saw palmetto occurred in only two of 100 tropical hardwood hammocks in Everglades National Park. The consistency with which saw palmetto was used by bobcats in this as well as other studies (Wassmer et al. 1988, Foster 1992), suggests that this is a very important component of bobcat habitat.

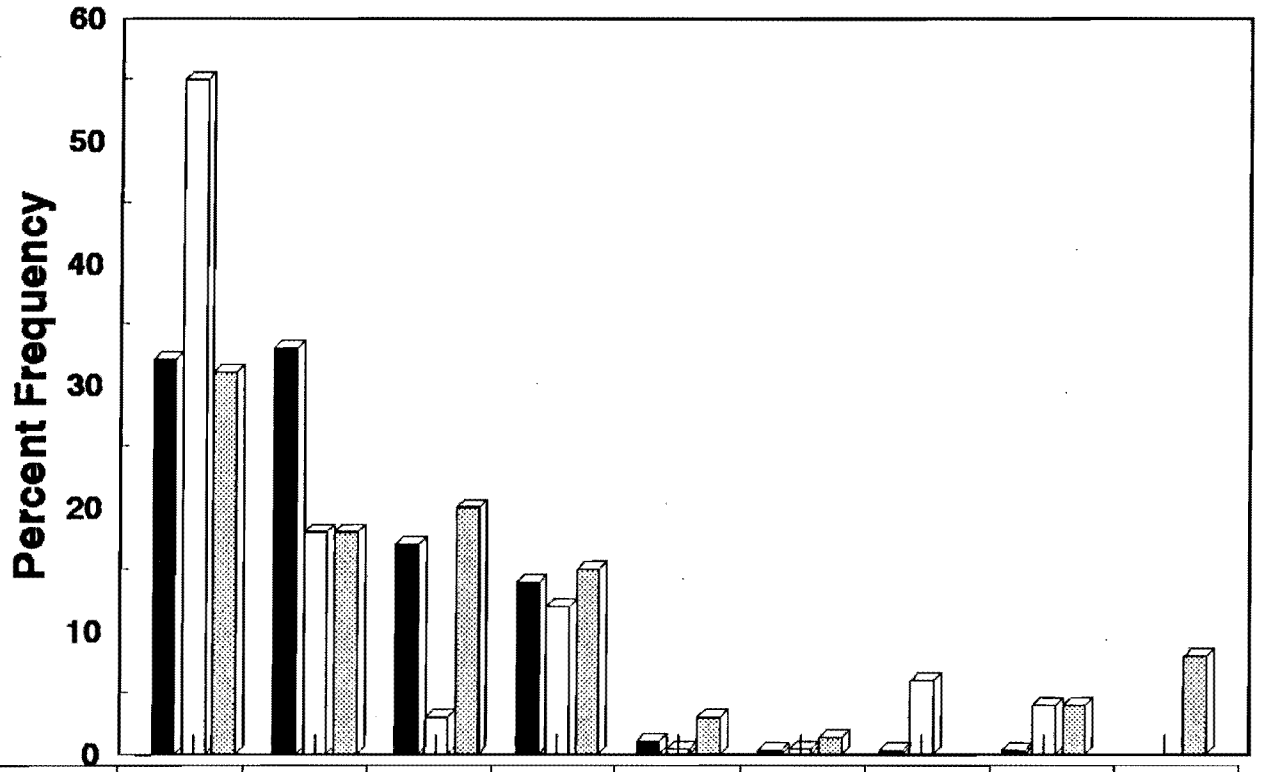
Measurements of dietary overlap indicated little likelihood of competition between any of south Florida's native carnivores. This was not the pattern, however, for measurements of habitat partitioning (Pianka 1986). While males and females from the same species usually exhibited close habitat affinities, black bears showed the least (0.75-0.87) similarities between gender (Table 3.11). Male and female panthers exhibited

Table 3.11. Seasonal habitat overlap (Pianka 1986) among large mammalian carnivores in south Florida.

Sex/species	F Bear	M Bear	F Bobcat	M Bobcat	F Panther	M Panther
			Winter			
F Bear	1					
M Bear	.815	1				
F Bobcat	.492	.723	1			
M Bobcat	.500	.639	.939	1		
F Panther	.800	.850	.630	.553	1	
M Panther	.697	.666	.690	.611	.907	1
			Summer			
F Bear	1					
M Bear	.751	1				
F Bobcat	.562	.749	1			
M Bobcat	.514	.685	.801	1		
F Panther	.845	.677	.591	.718	1	
M Panther	.725	.783	.740	.850	.945	1
			Fall			
F Bear	1					
M Bear	.875	1				
F Bobcat	.767	.913	1			
M Bobcat	.842	.955	.897	1		
F Panther	.965	.789	.671	.636	1	
M Panther	.960	.803	.696	.749	.957	1

overlap exceeding 0.90 in all seasons and portrayed a higher level of similarity than was suggested by factor analyses. Overlap ranged from a minimum of 0.49 between female bobcats and female black bears during winter, to a maximum of 0.96 between male panthers and female black bears during winter. Although few patterns were consistent in this analysis, and they did not universally agree with factor analyses, measurements based on the Pianka (1986) algorithm clearly demonstrated a high level of habitat overlap within this group of species. A predominantly vegetarian diet, different activity patterns, and winter denning allowed black bears to be involved in more high habitat overlap combinations than pairings between bobcats and panthers, which exhibited higher dietary overlap (see dietary overlap chapter). When gender was ignored, however, the importance of upland forests, and inland swamps to south Florida's large mammalian carnivores is obvious (Fig. 3.5).

The habitat overlap analysis (Table 3.11) supports the results of the factor analysis where some pairings of sympatric species exhibited greater overlap than gender within species. For example, female black bear habitat use was more similar to female panther habitat use during fall (0.965) than it was to male black bears (0.875). Some habitat use differences within species may be the product of evolutionary divergence that has reduced competition between the sexes. Sexual dimorphism occurs in all three species which, when combined with the behavior-altering influence of reproduction, may help to explain the observed patterns in habitat separation within species. While gender-dependent prey selection in bobcats and panthers may not be as dramatic as that reported in weasels (Mustela spp., Hall 1951, Lockie 1966, Erlinge 1974), and several bird species (Darwin 1871:208, Storer 1955, Selander 1966), even slight differences in prey selection may



Habitat Type	PP	HH	MS	CS	TS	MA	DP	AD	MG
Panther	32.0	33.0	17.0	14.0	1.0	0.3	0.3	0.3	0.0
Bobcat	55.0	18.0	3.0	12.0	0.4	0.4	6.0	4.0	0.0
Black bear	31.0	18.0	20.0	15.0	3.0	1.4	0.0	4.0	8.0

Figure 3.5. Annual habitat use patterns ignoring gender and season for large mammalian carnivores in south Florida.

dampen the effects of periodic prey scarcity or allow the predator's population to increase during times of prey abundance. Prey selection differences between male and female bears are likely insignificant despite their high degree of sexual dimorphism. Differences in food habits among south Florida's native carnivores may be sufficient to trivialize the extensive habitat overlap that they demonstrate. But for the two cat species in south Florida, prey selection may be an important factor explaining the differences in habitat use between the sexes.

CHAPTER 4

HABITAT PATTERN AROUND FLORIDA PANTHER NATAL DENS AND BLACK BEAR WINTER DENS

Natural history studies of Florida panthers and black bears in south Florida have examined habitat use (Belden et al 1988, Maehr et al. 1991a, Maehr et al. 1992), food habits (Maehr et al. 1990a), dispersal (Maehr et al. 1988), mass growth (Maehr and Moore 1992), and activity (Maehr et al. 1990b). Some aspects of female panther reproductive behavior were described by Maehr et al. (1989a, 1989b), but habitat descriptions of natal dens were limited to qualitative comparisons with day-use sites. There is a paucity of published literature pertaining to black bear ecology in south Florida. Given the importance of reproduction to population growth and stability in panthers (Maehr and Caddick 1995) and other large carnivores (Caughley and Sinclair 1994), a better understanding of natal den selection is important for promoting improved management practices in occupied panther range, in assessing reintroduction sites, and in managing habitat for black bears. This chapter describes the habitat characteristics at Florida panther natal dens and black bear winter dens, and examines the landscape context surrounding these critically important areas.

Study Area and Methods

Female Florida panthers were captured using trained hounds to tree the animals, removing them with anesthetic and "crash bags" (McCown et al. 1990), and then fitted with radio transmitters (150-152 MHz, Telonics, Inc., Mesa, AZ). Black bears were captured with culvert traps (Erickson 1957) or spring-activated snares, and both species were anesthetized with Ketamine hydrochloride administered from a compressed air gun or with a jab pole at a dosage of approximately 20 mg/kg of estimated body mass. Panthers were monitored three times per week, and black bears were monitored three times every two weeks, from fixed wing aircraft. Universal Transverse Mercator points were recorded for each location. Denning of panthers coincided with parturition and was predicted to occur approximately 90 days after an interaction with an adult male, or denning behavior was signaled by sharply restricted movements to localized parts of their home ranges. Black bear denning was indicated by repeated locations of an individual at one site during the four- month period, January-April. Panther natal dens were examined after females abandoned these sites with their two-month-old kittens, or when kittens were less than two weeks of age and the female was known to be away from the den. Winter black bear den locations were determined by radio telemetry, and some were examined for evidence of reproduction and the recording of habitat characteristics.

SPANS geographic information system (GIS) software (Tydac 1991) was used to analyze habitat variables derived from Thematic Mapper 30m Landsat imagery. The application of these data to a variety of Florida wildlife species was described by Cox et al. (1994), and was used to develop a statewide strategy for conserving wildlife habitat in

Florida. Coverage of vegetation was examined within 100m, 500m, 1000m, and 5000m radius circles around both winter and natal dens. Chi-square contingency tables ($p=0.05$) were used to evaluate differences in habitat distribution between 100m- and 1000m-radius circles around dens, and to evaluate the null hypothesis that habitat composition did not change with increased radius around den sites. Habitat types included pine flatwoods, hardwood hammock, herbaceous marsh (salt and fresh water), cypress swamp, mixed swamp, thicket swamp, mangrove swamp, dry and wet prairies, agricultural/disturbed, barren, and open water. Detailed descriptions of these vegetation types and the subtropical climate can be found in Davis (1943), and Maehr et al. (1991a). Analysis-of-variance was used to examine differences in the amount of forested habitat within the 4 distance zones around each den. When a significant difference ($p \leq 0.05$) was found, Duncan's multiple range test ($p=0.05$) was used to differentiate means. Distance from dens to the nearest paved road were measured using SPANS. These were then compared with an equal number of radio locations that were randomly selected from within the home range of each study animal during the year that denning was documented. Because black bears do not leave natal dens during winter, telemetry locations collected during the months of January through April were eliminated from the selection of random locations because most coordinates for this time period would be the den itself.

Results and Discussion

Habitat composition around 31 den sites was examined for 11 female Florida panthers between 1986 and 1995, 16 den sites of 13 adult female black bears between 1992 and 1994, and eight den sites of six male black bears between 1992 and 1993.

Although one Florida panther (#11) and one black bear (F03) were known to reuse a den site, none of the other individuals in this study exhibited loyalty to a single location. Thus, such biases likely had little influence on the independence of the sample. Dens of most panthers (67%) were located in thickets of saw palmetto (Maehr et al. 1990) or they were found in mixed swamp vegetation and hardwood hammocks. When occurring in these situations, den sites were hidden by thick ferns or saw palmetto, respectively. Virtually all panther dens were located within the area of 'highest probability' habitat as described by Maehr and Cox (1995:1014), and described as the habitat core in the concluding chapter of this dissertation. None of the black bear dens were found in hardwood hammocks, and female bears were the only group that utilized mangroves for denning. Most (58%) of the black bear dens were located in either pine flatwoods with a saw palmetto understory, or in mixed swamp vegetation. In the latter situation, elevated tree stumps, naturally low water conditions, or artificial drainage provided dry den sites.

Descriptions of cougar dens in North America are sparse. None of five recent ecological studies of cougars described natal den habitat, although descriptions of neonate kittens were made (Anderson 1983, Ashman et al. 1983, Hopkins 1989, Sweanor 1990, Jalkotzy et al. 1992). Dixon (1982:714), however, suggested that cougar natal areas were "rather simple den sites..., with only enough cover to keep out heavy rain and the hot sun." In mountainous settings they tend to be located in rocky cover, whereas thick vegetation is used elsewhere (Dixon 1982). Florida panther natal dens are typical of non-mountainous settings.

Black bears utilize a wide variety of structures for winter dens, ranging from snow ledges, rock caverns, hollow trees, ground excavations, elevated tussocks, hollow logs, thick brush, simply on the ground, and even beneath cabins (Willey 1978, Beck 1991, Erickson 1964, Jonkel and Cowan 1971, Johnson and Pelton 1979, Hellgren and Vaughan 1989, Hamilton and Marchinton 1980, Wooding and Hardisky 1992, Kolenosky and Strathearn 1987, Beecham et al. 1983, Hellgren and Vaughan 1989). Although Lindzey and Meslow (1976a) found that aspect did not influence den selection, several studies in mountainous areas have found that elevation, prevailing wind, and aspect were important to den selection in mountainous areas (LeCount 1983, Schwartz et al. 1987, Mack 1990). In some areas, excavated dens had sealed entrances (Kolenosky and Strathearn 1987). In south Florida, only one natal den located in the stump of a hollow cypress (Taxodium distichum) provided a barrier to wind or observation, and was the only den that was repeatedly used by the same female for subsequent litters. All others were located on the ground within a clump of vegetation.

Contingency tables indicate that significant differences exist in habitat distribution between 100m and 1000m distances around 87% of panther natal dens (Table 4.1). Similarly, the majority (79%) of black bear dens exhibited differences in habitat distribution between 100m and 1000m distances around dens (Tables 4.2 and 4.3). However, a subset of 6 maps created from these analyses misrepresented several cover types. This stemmed from the inability of SPANS to differentiate some forested habitats, so further analyses combined all forest cover into one class. The method of landcover analysis used by Cox et al. (1994) was sufficient to describe large-scale patterns in wildlife

Table 4.1. Contingency tables of percent frequency of habitat types surrounding Florida panther natal dens within a 100 m radius and a 1 km radius. Numbers in parentheses represent habitat composition within 1 km radius of den site. Probabilities in bold face are not significant (P>0.05)

		Habitat type[1]										
Cat#	**Year**	**PP**	**HH**	**FM**	**CS**	**MS**	**AD**	**BA**	**WA**	**TS**	**Chi[2]**	**Prob**
09	1987	2.7	0	0	97.3	0	0	0	0	0	18.17	0.006
		(20.5)	(0.9)	(1.2)	(77.3)	0	(0.04)	(0.1)	0	0		
09	1988	0	2.7	0	0	97.3	0	0	0	0	27.84	<.001
		0	(29.4)	0	(0.98)	(69.6)	0	0	0	0		
09	1990	0	10.8	0	0	89.2	0	0	0	0	82.87	<.001
		0	(35.9)	(14.3)	(23.3)	(27.4)	0	0	0	0		
11	1986	0	32.4	2.7	0	64.9	0	0	0	0	65.98	<.001
		(0.4)	(37.3)	(42.1)	(2.6)	(17.2)	(0.1)	(0.1)	0	0		
11	1988	0	32.4	2.7	0	64.9	0	0	0	0	65.98	<.001
		(0.4)	(37.3)	(42.1)	(2.6)	(17.2)	(0.1)	(0.1)	0	0		
11	1990	0	56.8	0	16.2	27.0	0	0	0	0	43.12	<.001
		(1.2)	(34.1)	(23.4)	(4.6)	(30.6)	(4.3)	(1.9)	0	0		
11	1991	13.5	10.8	0	5.4	62.2	5.4	2.7	0	0	80.78	<.001
		(33.5)	(15.7)	(5.1)	(12.1)	(4.8)	(26.2)	(1.5)	(0.6)	0		
11	1993	0	48.6	16.2	0	35.1	0	0	0	0	25.43	<.001
		(1.0)	(38.9)	(43.3)	(1.9)	(14.4)	(0.2)	(0.1)	0	0		
14	1989	0	8.1	91.9	0	0	0	0	0	0	**4.93**	**0.085**
		0	(2.4)	(95.8)	0	0	0	0	0	0		
19	1988	8.1	32.4	2.7	54.0	0	2.7	0	0	0	62.07	<.001
		(20.5)	(16.6)	(7.7)	(17.6)	(5.5)	(21.0)	(2.1)	0	0		
19	1989	0	70.3	0	29.7	0	0	0	0	0	35.21	<.001
		(0.4)	(59.6)	(2.3)	(12.8)	(24.3)	(0.4)	(0.2)	0	0		
19	1990	10.8	10.8	0	78.4	0	0	0	0	0	56.98	<.001
		(16.1)	(8.6)	(1.5)	(35.6)	(0.1)	(24.7)	(13.3)	0	0		
19	1992	2.7	35.1	0	62.2	0	0	0	0	0	38.31	<.001
		(3.7)	(5.6)	(15.4)	(75.2)	0	0	0	0	0		
19	1994	8.1	48.6	2.7	16.2	24.3	0	0	0	0	**6.505**	**0.482**
		(14.1)	(45.8)	(2.8)	(19.3)	(15.4)	(0.6)	(0.9)	(1.1)	0		
31	1989	13.5	0	0	51.3	0	0	35.1	0	0	40.45	<.001
		(15.4)	0	0	(43.6)	0	(28.0)	(11.8)	(0.04)	0		
31	1990	0	0	0	100.0	0	0	0	0	0	53.13	<.001
		(11.1)	(5.3)	(4.2)	(58.0)	0	(14.6)	(6.5)	(0.1)	0		
31	1991	18.9	35.1	0	37.8	5.4	2.7	0	0	0	64.05	<.001
		(15.1)	(15.0)	(6.9)	(13.2)	(5.1)	(30.0)	(4.4)	(9.5)	0		
32	1989	43.2	0	0	56.8	0	0	0	0	0	27.25	<.001
		(35.6)	(0.04)	(1.5)	(40.0)	0	(14.0)	(8.1)	0	0		
32	1992	27.0	2.7	0	70.3	0	0	0	0	0	19.07	.0019
		(24.2)	(14.5)	(5.9)	(52.9)	(1.1)	0	(1.3)	0	0		
36	1990	40.5	18.9	0	24.3	16.2	0	0	0	0	24.89	.0003
		(33.8)	(9.1)	(6.4)	(45.5)	(4.2)	(0.8)	(9.3)	0	0		
36	1991	89.2	2.7	0	0	5.4	2.7	0	0	0	102.49	<.001
		(20.0)	(4.1)	(0.9)	(34.5)	(23.7)	(7.4)	(9.3)	0	0		
36	1993	0	0	0	32.4	67.6	0	0	0	0	70.96	<.001
		(0.1)	(8.9)	(5.0)	(57.3)	(13.9)	(14.2)	(0.6)	0	0		

Table 4.1 (continued).

Cat#	Year	PP	HH	FM	CS	MS	AD	BA	WA	TS	Chi^2	Prob
40	1990	5.4	0	8.1	86.5	0	0	0	0	0	10.02	.0401
		(14.8)	(2.3)	(12.9)	(69.6)	(0.4)	0	0	0	0		
40	1992	37.8	2.7	16.2	43.2	0	0	0	0	0	3.641	.7251
		(29.1)	(1.0)	(23.9)	(45.9)	0	(0.1)	(0.04)	(0.04)	0		
40	1993	37.8	2.7	8.1	51.3	0	0	0	0	0	8.75	.1878
		(21.6)	(2.2)	(12.8)	(61.0)	(0.3)	(0.8)	(1.3)	0	0		
48	1993	10.8	21.6	29.7	37.8	0	0	0	0	0	23.09	.0016
		(7.0)	(13.5)	(25.6)	(34.1)	(2.3)	(13.3)	(1.6)	0	0		
48	1995	32.4	0	32.4	35.1	0	0	0	0	0	50.00	<.001
		(15.2)	(3.3)	(17.7)	(27.8)	(1.7)	(25.0)	(8.4)	(0.2)	0		
52	1993	0	81.1	0	0	0	0	0	0	18.9	87.76	<.001
		(1.2)	(19.4)	(11.9)	(3.1)	0	(27.0)	(1.7)	(0.04)	(35.4)		
52	1994	0	100	0	0	0	0	0	0	0	72.44	<.001
		(0.2)	(46.8)	(4.1)	(11.1)	0	(0.3)	(0.1)	0	(37.3)		
56	1994	54.0	0	8.1	37.8	0	0	0	0	0	15.73	.0153
		(30.5)	(0.9)	(20.7)	(45.9)	(0.1)	(1.0)	(0.9)	0	0		
56	1995	0	0	0	97.3	0	2.7	0	0	0	80.64	<.001
		0	(29.4)	(2.1)	(38.1)	(4.7)	(25.5)	(0.2)	0	0		
Means		14.7	21.5	7.1	36.2	18.0	0.5	1.2	0	0.6	16.15	.0402
		(12.5)	(17.5)	(14.8)	(31.2)	(9.2)	(9.0)	(2.8)	(0.4)	(2.3)		

[1]Abbreviations stand for the following habitat types: PP= pine flatwoods, HH= hardwood hammock, FM= freshwater marsh & wet prairie, CS= cypress swamp, MS= mixed swamp, AD= agricultural/improved pasture & disturbed, BA= barren, WA= open water, TS= thicket swamp.

Table 4.2. Contingency tables of percent frequency of habitat types surrounding female black bear winter dens within a 100 m radius and a 1 km radius. Numbers in parentheses represent habitat composition within 1 km radius of den. Probabilities in bold face are not significant (P>0.05).

		Habitat type[1]											
ID#	**Year**	**PP**	**HH**	**MA**	**CS**	**MS**	**TS**	**MG**	**WA**	**AD**	**BA**	X^2	**Prob**
F02	1992	0	54.0	29.7	0	16.2	0	0	0	0	0	24.0	.0004
		(0)	(27.0)	(52.7)	(2.6)	(12.3)	(0)	(0)	(0.4)	(2.3)	(2.8)		
F03	1993	0	48.6	0	0	32.4	0	0	0	0	18.9	24.4	.0004
		(0)	(37.9)	(0)	(0)	(60.5)	(0)	(0)	(0)	(0)	1.6		
F04	1992	0	56.8	0	35.1	8.1	0	0	0	0	0	13.1	**0.159**
		(0.2)	(67.0)	(2.3)	(15.5)	(14.7)	(0)	(0)	(0)	(0.2)	(0)		
F04	1993	0	78.4	0	5.4	16.2	0	0	0	0	0	11.5	**0.244**
		(0.4)	(64.7)	(3.1)	(15.2)	(13.7)	(0)	(0)	(0)	(0)	(1.8)		
F06	1993	24.3	2.7	0	51.3	0	0	0	0	13.5	8.1	6.9	**0.644**
		(25.6)	(1.9)	(0)	(59.2)	(0)	(0)	(0)	(0)	(3.4)	(9.8)		
F08	1992	0	0	0	100	0	0	0	0	0	0	31.4	<.001
		(9.0)	(5.9)	(0.4)	(72.9)	(0)	(0)	(0)	(0)	(4.7)	(7.2)		
F08	1993	0	0	0	100	0	0	0	0	0	0	49.8	<.001
		(7.6)	(4.6)	(0)	(58.3)	(22.3)	(0)	(0)	(0)	(0)	(4.3)		
F09	1992	0	0	16.2	0	0	0	83.8	0	0	0	28.6	0.001
		(0)	(1.7)	(41.8)	(0)	(0)	(0)	(49.6)	(1.7)	(0.1)	(5.0)		
F09	1994	0	0	67.6	0	0	0	32.4	0	0	0	19.9	.018
		(0)	(0.1)	(36.4)	(0)	(0)	(0)	(62.7)	(0.8)	(0)	(0)		
F10	1994	2.7	89.2	5.4	0	0	0	0	0	0	2.7	81.7	<.001
		(1.3)	(31.9)	(30.0)	(7.2)	(28.8)	(0)	(0)	(0)	(0)	(0.8)		
F11	1993	0	5.4	35.1	59.5	0	0	0	0	0	0	18.6	0.029
		(3.3)	(10.8)	(12.0)	(73.1)	(0.6)	(0)	(0)	(0)	(0)	(0.1)		
F12	1993	0	21.6	0	0	78.4	0	0	0	0	0	34.6	<.001
		(0)	(16.9)	(0)	(0)	(53.6)	(0)	(29.3)	(0)	(0)	(0.1)		
F13	1993	40.5	10.8	0	35.1	0	0	0	0	0	10.8	6.86	**0.652**
		(25.6)	(7.6)	(0)	(50.3)	(0)	(0)	(0)	(0)	(0)	(13.2)		
F15	1993	0	54.0	29.7	0	16.2	0	0	0	0	0	24.0	0.004
		(0)	(27.0)	(52.7)	(2.6)	(12.3)	(0)	(0)	(0.4)	(2.3)	(2.8)		
F17	1994	13.5	0	0	37.8	0	0	0	0	0	48.6	26.1	0.002
		(19.5)	(1.3)	(0)	(54.5)	(0)	(0)	(0)	(0)	(6.6)	(18.0)		
F19	1994	24.3	8.1	5.4	27.0	0	0	0	0	0	29.7	41.3	<.001
		(10.7)	(3.9)	(2.5)	(66.3)	(4.6)	(0)	(0)	(0)	(0)	(8.1)		
Means		6.6	26.8	11.8	28.2	10.5	0	7.3	0	0.8	7.4		
		(6.4)	(19.4)	(14.6)	(29.8)	(14.0)	(0)	(8.8)	(0.2)	(1.2)	(4.7)		

[1]PP=pine flatwoods. HH=hardwood hammock, MA=herbaceous marsh, CS=cypress swamp, MS=mixed swamp, TS=thicket swamp, MG=mangrove swamp, WA=open water, AD=agricultural/disturbed, BA=barren.

Table 4.3. Contingency tables of percent frequency of habitat types surrounding male black bear winter dens within a 100 m radius and a 1 km radius. Numbers in parentheses represent habitat composition within 1 km radius of den. Probabilities in bold face are not significant (P>0.05).

		Habitat type[1]											
ID#	Year	PP	HH	MA	CS	MS	TS	MG	WA	AD	BA	X^2	Prob
M08	1992	10.8	2.7	32.4	29.7	0	0	0	0	0	0	38.6	<.001
		(5.5)	(8.1)	(12.7)	(72.1)	(0)	(0)	(0)	(0.2)	(0)	(0.2)		
M08	1993	0	24.3	0	70.3	5.4	0	0	0	0	0	23.9	0.004
		(6.8)	(9.7)	(5.2)	(78.1)	(0.1)	(0)	(0)	(0)	(0)	(0.1)		
M11	1992	43.2	0	0	56.8	0	0	0	0	0	0	25.2	0.003
		(19.1)	(2.8)	(0)	(65.7)	(0)	(0)	(0)	(0)	(2.7)	(9.7)		
M13	1992	13.5	0	0	0	0	0	0	0	86.5	0	91.8	<.001
		(57.8)	(0.8)	(9.9)	(0.6)	(0)	(0)	(0)	(0.1)	17.8	(7.7)		
M13	1993	0	48.6	51.3	0	0	0	0	0	0	0	114	<.001
		(13.5)	(0.6)	(35.0)	(0)	(0)	(2.0)	(24.2)	(4.5)	(5.7)	(14.5)		
M14	1992	13.5	0	0	18.9	0	0	0	0	43.2	24.3	6.6	**0.675**
		(17.4)	(1.4)	(1.0)	(26.0)	(0)	(0)	(0)	(0)	39.7	(14.5)		
M20	1993	0	0	51.3	48.6	0	0	0	0	0	0	24.1	0.004
		(7.1)	(9.0)	(33.6)	(46.1)	(1.8)	(0)	(0)	(0)	(1.2)	(1.2)		
M33	1993	10.8	2.7	0	62.2	0	0	0	0	5.4	18.9	24.8	0.003
		(10.6)	(3.5)	(0.1)	(69.2)	(11.1)	(0)	(0)	(0)	(2.9)	(2.6)		
Means		11.5	9.8	16.9	35.8	0.7	0	0	0	16.9	5.4		
		(17.2)	(4.5)	(12.2)	(44.7)	(1.6)	(0.2)	(3.0)	(0.6)	(8.7)	(6.3)		

[1]PP=pine flatwoods. HH=hardwood hammock, MA=herbaceous marsh, CS=cypress swamp, MS=mixed swamp, TS=thicket swamp, MG=mangrove swamp, WA=open water, AD=agricultural/disturbed, BA=barren.

Table 4.4. Proportion of forested cover within circular areas around Florida panther natal den sites, 1986-1995. Means followed by different letters are significantly different (Duncan's multiple range test, P=0.05).

Circle radius	Area (km^2)	Proportion forested
100m	0.03	94.1 A
500m	0.78	83.9 B
1000m	2.35	75.7 C
5000m	75.21	68.5 D

habitat from a statewide perspective, and is a valuable tool for illustrating these patterns. However, when the same satellite image was used to describe habitat patterns at the finer scale in this analysis, inconsistencies in the data were magnified. Although this precluded further analysis to determine key landscape variables based on specific plant communities, Maehr and Cox (1995) found that distribution of forest cover, regardless of forest type, was correlated with the distribution of radio telemetry locations of all panthers in south Florida.

A significant difference ($F=18.8$, $p<0.001$) was found among the means of percent forest cover between 100m, 500m, 1000m, and 5000m radius circles around all panther den sites (Fig. 4.1). Areas of increasingly larger size contained proportionally less forest cover than the next smallest area (Table 4.4). Although habitat characteristics around den sites varied among individual panthers, only 6% (n=2) exhibited more percent forest in the 500m circle than in the 100m circle. In no instance did 1000m or 5000m circles contain proportionally more forest than 100m circles. No significant differences were found in the proportion of forest cover among radial distances areas around male black bear dens ($F=0.244$, $p=0.865$, $df=3$), and female black bear dens ($F=0.351$, $p=0.789$, $df=3$). Forest cover within the 100m radius area around individual bear dens ranged from 13.5% to 100%, and no trend in coverage was apparent in larger areas.

Clearly, selection of natal and winter den sites is influenced not only by available habitat, but also by species, sex, and individual preferences. Interestingly, only one panther (female #11, 1986, 1988) and one bear (female F03, 1993, 1995) were known to reuse a den location. Even though it was not possible, within the confines of this study, to measure all individual tendencies, a decrease in forest cover with increasing distance from

Table 4.5. Frequency of occurrence of known primary cover type at Florida panther natal dens, and winter dens of female and male black bears in south Florida, 1986-1994.

	Habitat type[1]						
Den type	PP	HH	CS	MS	TS	MG	AD
Panther	18	5	1	3	-	-	-
F bear	5	-	2	7	-	2	-
M bear	1	-	4	1	1	-	1

[1]PP=pine flatwoods. HH=hardwood hammock, CS=cypress swamp, MS=mixed swamp, TS=thicket swamp, MG=mangrove swamp, AD=agricultural/disturbed.

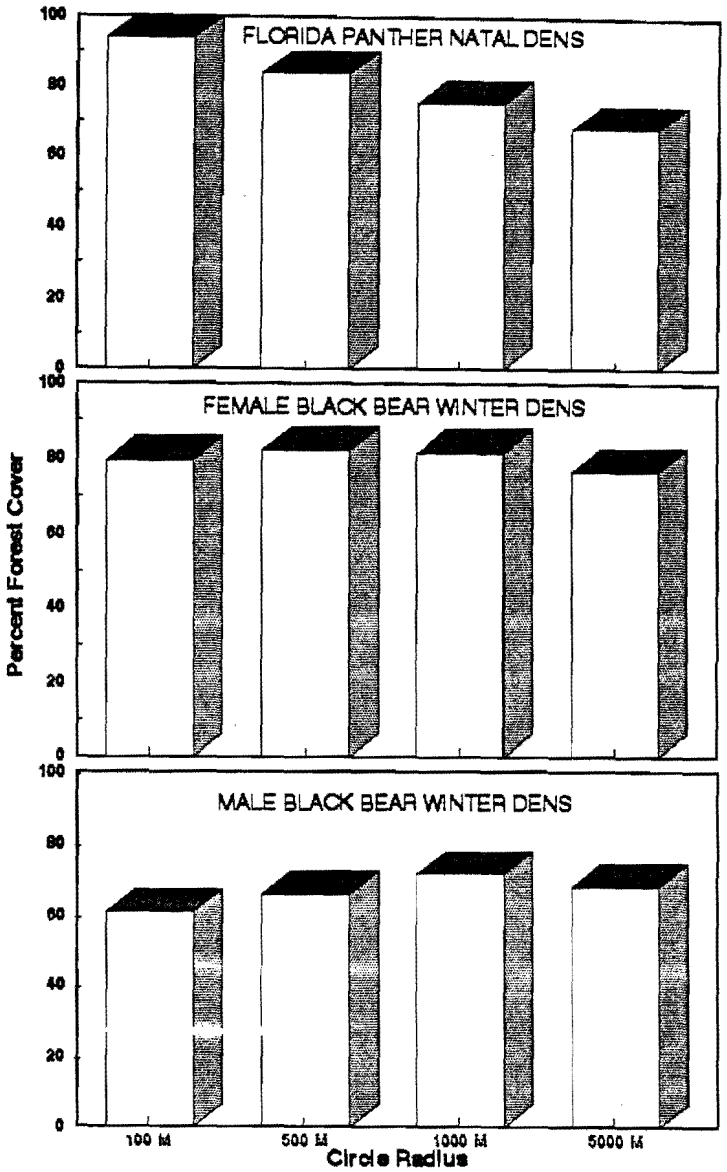


Figure 4.1. Change in percent forest cover with increasing radial distance away from panther natal dens, black bear natal dens, and male black bear winter dens in south Florida.

the den was a consistent pattern among panthers. While male panthers have regularly used the entirety of known south Florida panther range (Maehr et al. 1991a, 1992), no reproducing females have been documented in the northern reaches of this area. This begs the question of whether the reduced amount of forest cover provides female panthers with conditions conducive to den selection and kitten rearing.

Black bears, on the other hand, appear much more general in their den requirements inasmuch as no single cover type is clearly preferred (Table 4.5), nor does the amount of forest cover with increasing distance from den sites change. A slight increase in the amount of forest cover in the 500m and 1000m areas around male and female dens suggests that black bears may be more tolerant of forest edges for den sites than are panthers. Further, denning male black bears seem to tolerate areas with less forest cover than denning females. Some of the areas used by black bears were fragmented by natural influences such as tidal flowways through mangroves, or they were artificially altered by agriculture. As was noted in the food habits chapter, many black bear foods such as colonial ants (Crematogaster pilosa), and emergent plants such as alligator flag (Thalia geniculata) are typical in open, unforested settings, and energetic advantages may exist where such feeding areas are adjacent to dens. Shorter travel to obtain food upon den emergence of bear families or of males making periodic winter forays would help conserve and replenish stored energy reserves.

South Florida simply does not offer uniform forest conditions to panthers. When female panther dens from eastern Big Cypress National Preserve and Everglades National Park (n=3) are included with all south Florida dens documented between 1986 and 1995,

the importance of uninterrupted forest cover is compelling. Out of 33 known successful dens, 91% occurred in a continuous band of forest that is contained within three public preserves (only one of which is managed for panthers), an Indian reservation, and an array of bordering private lands. It is also of interest that although the majority of successful dens were associated with this narrow band of forest, their locations do not exhibit a tendency to be centrally located within it. Indeed, many appear to occur near the edges of this landscape feature. Dens located near forest edges may provide females with better hunting conditions than may be available within the center of the habitat core, especially when they have greatly reduced their home ranges when raising young kittens (Maehr et al 1989a). Regardless, large, uninterrupted expanses of forest are implicated in consistent panther reproduction.

Female #14 resided in Everglades National Park, and may provide some additional insight into the value of forest to panthers. Her successful 1989 den was typical of most panthers when examined within the confines of the 100m radius circle surrounding it (i.e. 100% forest cover). However, forest cover dropped from 4.2% to less than 3% in the 500m to 5000m radii. Apparently, relatively small patches of forest can facilitate successful reproduction, but when the surrounding landscape is dominated by herbaceous vegetation, the persistence of the local population remains doubtful even when kittens are successfully raised. Bass and Maehr (1991) observed that insufficient forest cover may have contributed to the most recent extinction of panthers in the Everglades. Further, the two successful dens in eastern Big Cypress Swamp (which also occurred in an area of sparse forest cover and natural fragmentation) have not contributed any individuals to the

core reproducing population of residents to the north and west. During the last 10 years the southeastern Florida landscape, which includes over 795,000 ha of public lands, has produced only three documented den sites versus 31 known dens in a more densely forested area of southwest Florida with many property owners but only 20% as large. This contrast reinforces the suggestion that the majority of the Big Cypress Swamp and the Everglades are panther population sinks that may occasionally accommodate overflow from the better habitat and population core, but do not in themselves contribute to the growth or stability of the overall population. Perhaps this is due in part to the lack of sufficient den habitat.

Figure 2 in Maehr and Cox (1995:1014) suggests that little panther habitat exists in Monroe and Dade counties south of the population core. To the north, agricultural activities and the dredged Caloosahatchee River artificially separate the core from the next largest concentration of continuous forest cover in Charlotte, Glades, and Highlands counties where owners of private ranches are reluctant to permit government-sponsored research. Nonetheless, panthers have been documented here during the last three decades, and analysis of Landsat imagery suggests that this disjunct region of south Florida is probably more capable of supporting reproduction than the habitat in most of the Big Cypress National Preserve and all of Everglades National Park. In this peripheral area of panther range, forest cover, although it is unnaturally fragmented, is more continuous than that found naturally in southeastern Florida.

Black bears are similar to panthers in exhibiting an aversion to the eastern Big Cypress Swamp and Everglades National Park, even though food availability during fall

may temporarily increase bear populations in these areas. Nonetheless, black bears seem less constrained by anthropogenic changes to the landscape and will use dens within areas of sparser forest cover than will panthers. The ability to negotiate obstacles such as the Caloosahatchee River has also been demonstrated by black bears (Maehr et al. 1988), but not by panthers. Further, the effective occupiable area for black bears is larger than that of panthers because bears use mangroves, and because they successfully give birth to and raise cubs in suburban areas such as the northern Golden Gate Estates where female winter dens have been located within one km of human residences.

The natural re-establishment of a panther population in south central Florida (north of the Caloosahatchee River) appears to be hindered by formidable landscape obstacles such as channelized rivers and lack of connecting forests. The relocation of subadult females directly from the south Florida population into this area may be the most practical way to determine the ability of this landscape to support panthers, and to reestablish a resident population. More widespread forest in this area (Maehr and Cox 1995) relative to the Everglades suggests that panthers may have a greater likelihood of persisting if re-establishment can occur. Ironically, the only significant parcel of public-owned land in this three-county area is the 25,293 ha Cecil Webb Wildlife Management Area, which is managed primarily for northern bobwhite (Colinus virginianus) hunting. Frequent prescribed fires and mechanical disturbances that are designed to arrest vegetative succession, and maintain an open forest canopy with light ground cover create conditions that are not conducive to panther occupation. In fact, the GIS analysis by Cox et al. (1994:67) reveals that this area is an inhospitable zone within a larger matrix of potential

panther habitat. Thus the intensive management practices employed on this tract of public land for the purposes of quail hunting may have reduced its value not only to panthers, but by reducing the density and distribution of saw palmetto, both denning and feeding habitat for black bears has been eliminated. Although the Cecil Webb Wildlife Management Area may not provide attractive conditions to Florida's native large carnivores today, it could certainly be restored as valuable denning and feeding habitat for both bears and panthers if current management practices changed from the artificial inhibition of succession to the encouragement of heavier patches of forest.

Influence of Roads

Although Maehr and Cox (1995) found a relation between landscape island size and panther distribution, even the largest landscape patches as defined by the lack of paved highways were virtually devoid of panthers. When habitat features are examined, however, it becomes clear that the largest roadless areas in south Florida are dominated by herbaceous wetlands such as sawgrass marsh, cypress savannas, and other unforested expanses. Thus, highways have little if any influence on their use by panthers. Inasmuch as Maehr et al. (1991a) observed that resident adult females avoided use of areas with paved highways, it seemed reasonable that this influence might also extend to the selection of den sites. Little is known about the influence of roads on Florida black bear behavior, however Beringer et al. (1990) found that interstate highways in North Carolina were crossed with lower frequency by bears than were smaller highways with less traffic.

Distances from locations to highways were calculated for 30 panther den sites (Fig. 4.2), 25 black bear winter dens (Fig. 4.3), and a randomly selected point from each animal's home range during the year that denning occurred. Analysis of variance between

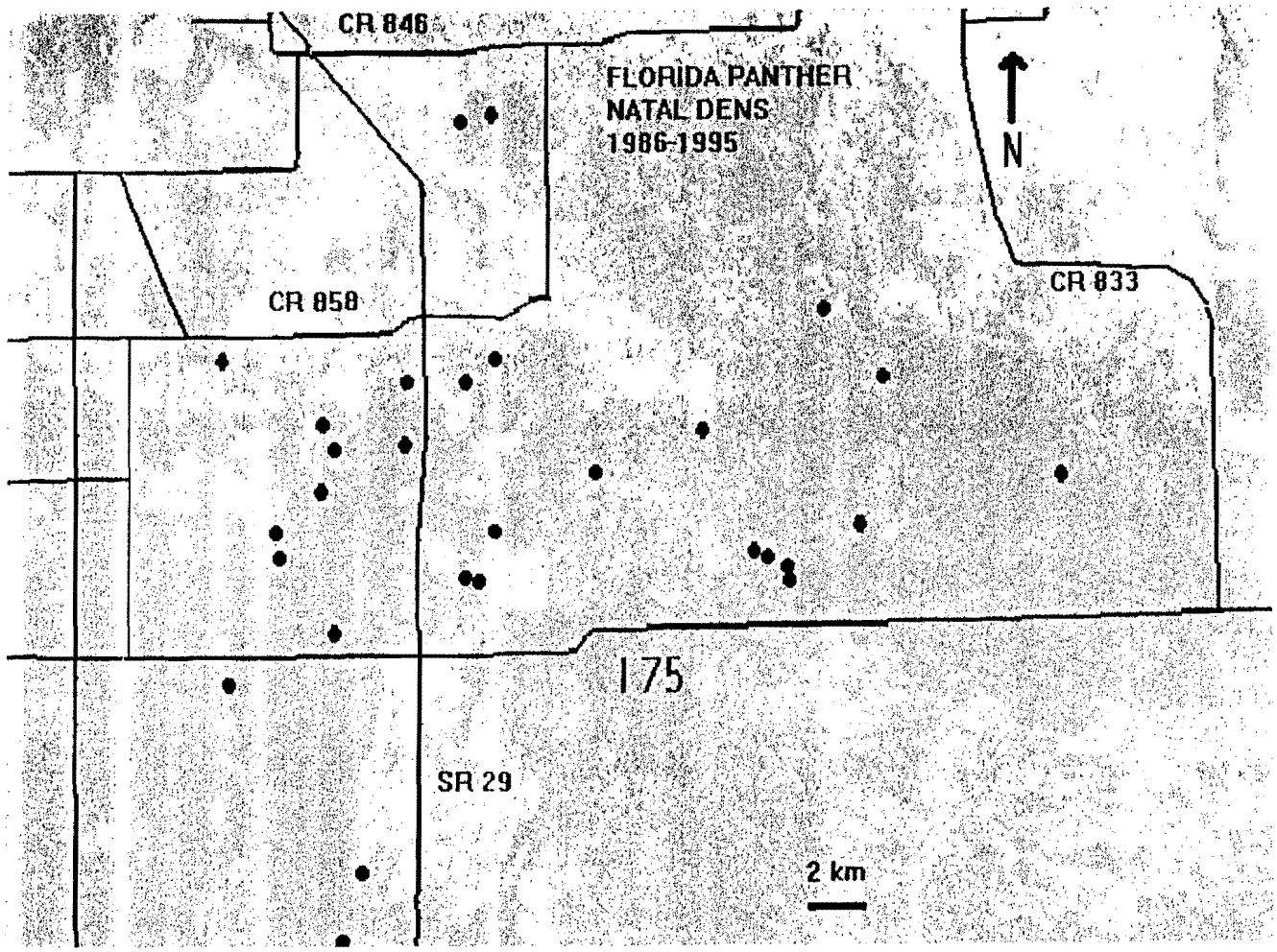


Figure 4.2. Distribution of Florida panther natal dens in south Florida, 1986 - 1995.

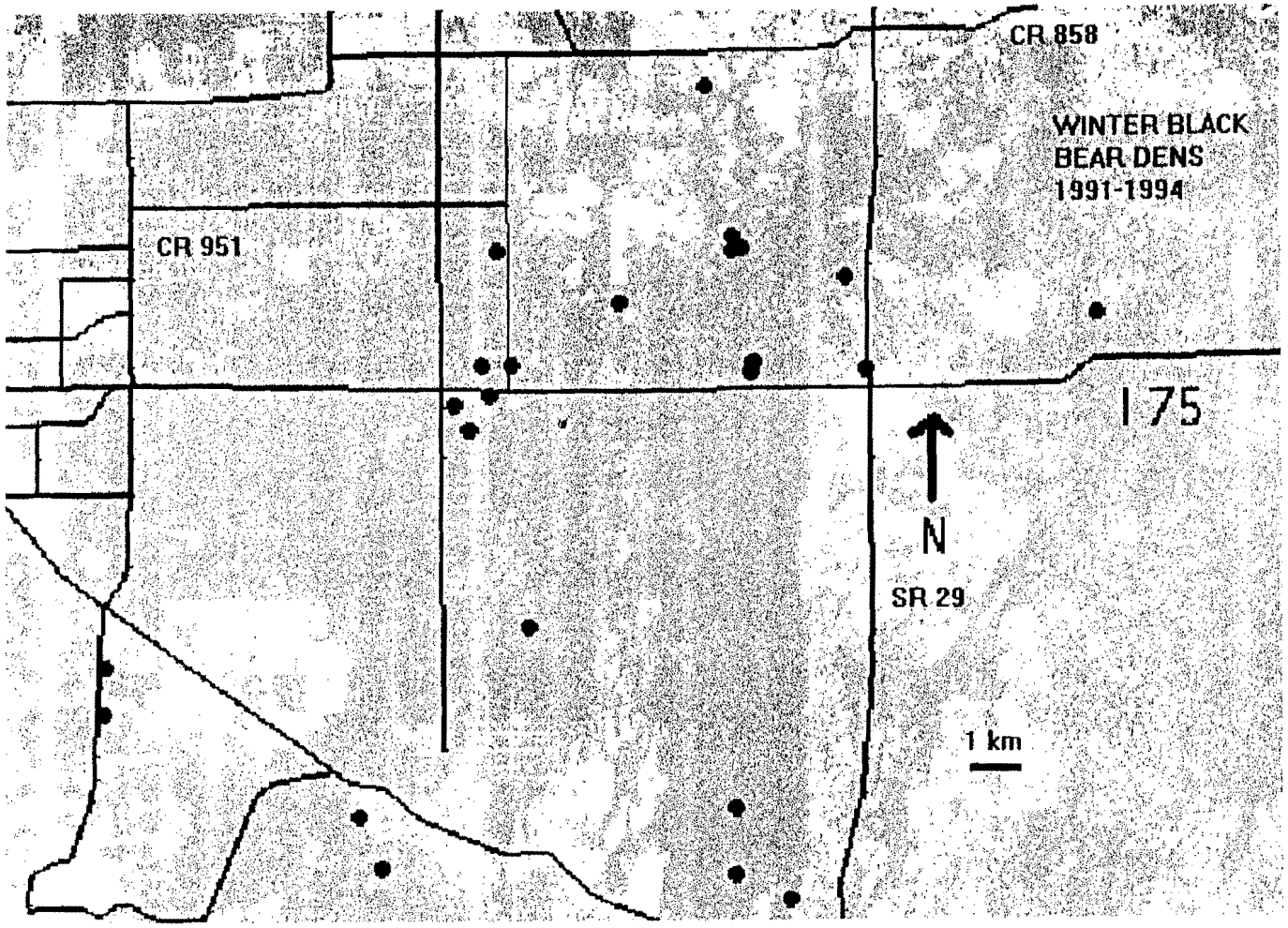


Figure 4.3. Distribution of black bear winter dens in south Florida, 1991 - 1994.

known dens and randomly selected points revealed no significant differences for panthers ($F=0.016$, $p=0.90$) or bears ($F=0.086$, $p=0.77$ for 16 female dens, $F=1.857$, $p=0.19$ for 9 male dens). However, despite similar means (4.1 vs. 4.2 km), panther den locations exhibited a much lower variance than randomly selected locations. Further, 100% of panther dens were located $\geq$1.0 km away from roads (range 1.0 to 11.2 km, sd=4.20), while 10% of the random locations were <1.0 km away (range 0.1-0.7). This suggests that resident female panthers tolerate some proximity to roads when not tending dependent kittens at the den, and that locations $\geq$1.0 km away from roads are chosen for den sites.

Black bear natal dens were found closer to highways than were panther dens ($F=8.32$, $p=0.006$). These distances ranged from 0.06 to 6.39 km (sd=2.02), and likely result from the black bear's tolerance to a wide variety of den situations. It may also be a result of smaller home range size and trap site locations. Because most trap sites were accessible by vehicle and close to roads, and because black bear home ranges are considerably smaller than panther home ranges (see home range and land tenure chapter), it is likely that females inhabiting interior forests such as the Fakahatchee Strand were not well represented in this sample. Thus, these data should not be interpreted to suggest that female black bears prefer den sites close to roads, but rather, that some bears are more likely to inhabit and den in areas that are closer to roads than are panthers. Most certainly, there are many south Florida black bears that routinely den as far away from roads as female panthers, but these individuals may not have been equally susceptible to capture.

These analyses indicate that black bears utilize more habitats for dens and tolerate more anthropogenic disturbances than do female panthers. Further, black bear numbers in south Florida should be expected to be much higher than panthers, not only because black bears have smaller home ranges, but because they seem more tolerant of highways than are panthers. Areas that panthers use only occasionally can also be readily used by female black bears that contribute to reproduction. This same zone, which appears to be a two km-wide band around paved highways, may reduce the potential population size of panthers in south Florida.

CHAPTER 5

HOME RANGE AND LAND TENURE

An expected behavior for most terrestrial carnivores is the maintenance of a familiar area that is used evenly throughout the year (Ewer 1968). Maehr et al. (1991) demonstrated that resident adult Florida panthers fit this stereotype by occupying the same area regardless of season. In some western locations, however, cougars have been shown to exhibit distinct seasonal home range shifts that coincide with snowfall and movements of prey (Seidensticker et al. 1973, Ashman et al. 1983, Logan and Irwin 1985). Similarly, bobcats demonstrate flexibility in home range utilization. Some populations respond to marked changes in resource availability (Rolley and Warde 1985, Toweill and Anthony 1988, Knick 1990, Koehler and Hornocker 1991) while others exhibit no seasonal shifts (Buie et al. 1979, Wassmer et al. 1988). In general, populations of bobcats and cougars that exist at higher latitudes demonstrate more distinct seasonal changes in home range than populations at lower latitudes.

Black bears, regardless of their geographic location, shift home ranges in response to changing food supplies (Lindzey and Meslow 1977a, Landers et al. 1979, Garshelis and Pelton 1981, Villarubia 1982, Klenner 1987, Doan-Crider 1995). Some of these shifts can be extensive. Rogers (1987a) recorded a non-dispersal fall movement >200 km for a male

in Minnesota. In addition, reproductive physiology in female black bears requires denning inactivity that can last several months (Jonkel and Cowan 1971, Lindzey and Meslow 1976a, Fuller and Keith 1980, LeCount 1983, Rogers 1987a, Hellgren and Vaughan 1989), and hibernation is a prerequisite for overwintering survival in most populations. Individuals living in Minnesota have remained in hibernation for up to 7 months (Rogers 1987a). On the other hand, some black bears in the southeastern United States remain active throughout the winter (Hamilton and Marchinton 1980). Rogers (1987a) has suggested that hibernation in black bears is an adaptation to an absence of food and is not a behavioral mechanism to avoid cold temperatures. Given the year-round availability of food, one would expect denning to be absent from south Florida bears. Latitude appears to be correlated with length of the denning period (Johnson and Pelton 1980, Hellgren and Vaughan 1989). Accordingly, individuals in the southern United States den for shorter periods, but a pulse of denning and winter parturition is universal among black bear populations regardless of latitude.

Most solitary mammalian carnivores follow a pattern of spatial arrangement known as land tenure, where standing residents have prior rights to their home ranges (Seidensticker et al. 1973). Maehr et al. (1991), and Maehr and Caddick (1995) suggested that Florida panthers maintain social and reproductive stability by living in a land tenure system. Such a system has resulted in low resident adult turnover and limited dispersal success among panthers, especially males. Little work has examined land tenure in black bears. However, Rogers (1987a) found that adult females facilitated female offspring home range establishment by shifting their home ranges to accommodate

daughters. In addition, he found that resident adults reduced immigration opportunities for dispersing bears, especially males. These patterns are similar to land tenure in Felis concolor.

Bobcats exhibit great variability in spatial arrangement from high degrees of home range overlap between sexes, to gender segregation (McCord and Cardoza 1982, Anderson 1987). However, the highest densities occurred where bobcats maintained exclusive home ranges (Lembeck and Gould 1979, Miller and Speake 1979). Zezulak and Schwab (1979) suggested that intrinsic behavioral mechanisms similar to those of other felid species operated also in bobcats. Bailey (1974) introduced the concept of land tenure based on prior rights in Idaho bobcats, although the variation in social strategies that were documented in the other studies cited above complicate the creation of an overarching concept of bobcat social ecology. In Florida, Wassmer et al. (1988) found that female bobcat home ranges did not overlap and that these were generally encompassed by larger male home ranges. Foster (1992) observed a similar pattern in southwest Florida with little overlap within sexes, but occasional overlap between males and females.

Methods

I examined home range patterns among bobcats, black bears, and panthers in south Florida in order to determine the influence of season on the spatial arrangement of these species relative to each other and to conspecifics. Although seasonal variation in panther habitat use and diet has not been observed (Maehr et al. 1990a, Maehr et al. 1991), and bobcats appear to exhibit consistent annual movement patterns (Wassmer et al. 1988), bobcat diet varies seasonally in Florida (Maehr and Brady 1986). Seasons were based on

bear food phenology described in the dietary overlap chapter, where January-April was winter, May-August was summer, and September-December was fall. In addition, few studies have described the fates of long-standing resident carnivores, so I also examined the home range dynamics of individual Florida panthers relative to age of the resident and the status of same-sex neighbors in order to better understand the process of home range replacement.

Seasonal home ranges of adult resident bobcats, black bears, and Florida panthers were estimated using minimum convex polygons (Mohr 1947). Annual home ranges also were determined in order to make comparisons with other studies and to portray overlap with conspecifics and with other species. Resident black bears were at least three years of age or exhibited reproductive activity. Bobcats were considered residents if their movements exhibited a central tendency (Bailey 1972), and if their body mass exceeded nine kg (Crowe 1975). Maehr et al.(1991) classified Florida panthers as residents if "males were greater than years old, exhibited regular movement patterns over large home ranges, and overlapped with several adult females. Resident adult females were $\geq$18 months old, had small home ranges, overlapped with other adult females, and exhibited reproductive behavior (mating, denning, kitten-rearing)."

Analysis of variance was used to examine seasonal means of home range size among species/gender groups. If a significant difference ($P \leq 0.05$) among species/gender groups was found within a season, Duncan's multiple range test was used to differentiate means. Winter home range sizes of denning and non-denning black bears were compared using Student's t-test ($P=0.05$). Individual home range dynamics for adult panthers

monitored greater than three years were examined by calculating annual home ranges, and arithmetic home range centers of these home ranges. Home ranges were considered stable if arithmetic means displayed a subjectively determined central tendency. Abandonment occurred if a subsequent home range did not overlap with the home range from a previous year. A shift occurred if a subsequent home range center was at least one home range radius from the previous home range center.

Black bear activity was monitored with an automatic field data recording station. Pulse rate changes of motion-sensitive transmitters attached to black bears were recorded with a digitized data processor, receiver (TDP-2, TR-2; Telonics, Inc., Mesa, Ariz.), and chart recorder (Gulton Co., mod. 2W288, Manchester, N.H.). Stations were established within 100 m of dens, or as close to active bears as possible without influencing their behavior. Radio transmitters (Mods. 315, 500, 505, Telonics, Inc.) were equipped with motion-sensitive switches and variable pulse rates: about 70 pulses per minute head up, and about 60 pulses per minute head down. Activity rate was defined as the percentage of minutes within each hour containing a pulse rate change (Maehr et al. 1990b).

Results and Discussion

Between January 1986 and December 1994, eight adult bobcats (four females, four males), 25 adult panthers (13 females, 12 males), and 30 adult black bears (14 females, 16 males) were monitored with radio-collars in southwest Florida (Table 5.1). All bobcats were captured as adults, whereas one female black bear, three female panthers, and four male panthers, were captured as dependent juveniles, or as independent subadults before they were monitored as adults. Ten Florida panthers were monitored for at least three

Table 5.1. Annual home range sizes of adult black bears, bobcats, and panthers in south Florida, 1986-1994. Years in bold type indicate denning for that individual.

ID#	Sex	Capture date	Home range year	Age (years) at first capture	Adult weight (kg)	Locations	Home range size (km^2)
Bears							
F02[1]	F	5/9/91	**1992**	7	101	81	40.5
F03[1]	F	8/15/91	1992	6	70.3	75	205.6
F04[1]	F	8/15/91	**1992**	6	63.5	80	40.7
F05[1]	F	9/20/91	1992	3	58.0	49	37.0
F07[1]	F	10/29/91	1992	9	88.4	81	21.9
F08[1]	F	11/5/91	**1992**	7	111.6	82	11.9
F09[1]	F	11/8/91	**1992**	3	77.1	82	17.7
F10[1]	F	11/14/91	1992	3	75.7	77	101.9
F11[1]	F	5/12/92	1992	3	63.5	70	73.0
F12[1]	F	6/1/92	1992	4	77.1	73	23.5
F13[1]	F	6/17/92	**1993**	4	81.6	76	43.2
F15[1]	F	10/25/92	**1993**	2	68.0	63	10.6
F17[1]	F	11/25/92	1993	6	90.7	76	98.1
F19[1]	F	12/16/92	1993	6	88.4	75	33.3
M03[1]	M	2/18/91	1991	3	147.4	74	311.0
M06[1]	M	8/8/91	1992	14	138.3	51	147.0
M08[1]	M	8/14/91	**1992**	5	104.3	77	125.5
M12[1]	M	9/25/91	1992	14	147.4	40	586.2
M13[1]	M	10/18/91	**1992**	3	154.2	81	159.3
M17[1,6]	M	1/19/92	1992	3	124.7	23	25.0
M18[1]	M	1/30/92	1992	12	220.0	68	362.1
M20[1]	M	2/7/92	**1993**	9	112.0	67	181.1
M24[1]	M	6/12/92	1993	4	163.3	82	418.8
M25[1]	M	7/30/92	1993	6	139.7	49	166.2
M28[1]	M	10/8/92	1993	3	97.5	84	647.7
M29[1]	M	10/8/92	1993	4	124.7	78	204.4
M36[1]	M	5/26/93	1993	9	165.6	72	305.0
M39[1]	M	7/28/93	1994	12	147.4	70	166.0
M41[1]	M	7/31/93	1993	5	104.3	35	228.6
M42[1]	M	8/12/93	1994	5	145.4	74	246.3
Panthers							
08[1,2]	F	3/25/84	1986	9-10	33.9	188	152.0
09[1]	F	1/26/85	1986	3-4	35.8	203	228.8
11[1]	F	1/21/86	**1986**	3-4	41.7	191	171.0
18[1,2]	F	1/22/87	1987	7-8	45.3	157	501.8
19[1]	F	2/9/87	**1989**	0.75	34.5	146	122.8

Table 5.1. (continued)

ID#	Sex	Capture date	Home range year	Age (years) at first capture	Adult weight (kg)	Locations	Home range size (km^2)
31[1]	F	1/12/89	1989	7-9	38.5	169	196.6
32[1]	F	2/3/89	1989	2-3	32.2	158	155.3
36[1]	F	1/27/90	1990	4-5	49.0	140	186.7
40[1]	F	2/26/90	1992	1-2	36.3	149	174.5
41[3]	F	2/28/90	1990	1-2	27.7	89	264.3
48[1]	F	2/24/92	1993	0.3	30.8	147	157.5
49[4]	F	2/25/92	1992	2-3	32.2	78	81.1
52[1]	F	5/5/92	1993	0.5	30.8	148	227.8
12[1]	M	1/28/86	1986	4-5	55.3	175	600.9
13[5]	M	2/27/86	1986	4-5	57.1	154	730.2
17[1]	M	1/20/87	1987	6-7	64.4	159	408.1
20[5]	M	3/10/87	1987	3-4	67.1	110	752.3
25[5]	M	2/16/88	1988	4-5	54.9	87	226.6
26[1]	M	3/1/88	1989	5-6	54.4	156	332.2
28[5]	M	11/29/88	1991	1.5	54.4	138	336.7
29[5]	M	1/3/89	1991	0.5	54.9	141	244.3
34[5]	M	1/8/90	1993	0.8	56.7	130	208.2
37[1]	M	1/30/90	1990	3-4	46.2	128	734.2
46[1]	M	1/30/92	1993	2-3	52.6	146	312.3
51[1]	M	3/26/92	1993	2-3	49.0	147	296.2
Bobcats							
M01[1]	M	3/1/86	1986	Adult		93	48.9
M02[1]	M	3/2/86	1986	Adult	10.0	95	17.8
M05[1]	M	9/1/86	1987	Adult		57	16.6
M08[1]	M	3/3/87	1987	Adult	12.7	32	66.9
F03[1]	F	3/17/86	1986	Adult		99	18.9
F06[1]	F	2/27/87	1986	Adult	10.2	34	7.0
F07[1]	F	2/25/87	1987	Adult	9.1	40	17.3
F09[1]	F	3/5/87	1987	Adult	10.4	20	12.7

[1]Resident adult
[2]Non-reproductive
[3]Killed before first litter
[4]Transmitter failed before first litter
[5]Non-resident adult
[6]Not used in calculation of mean

years (seven females, three males), and three of these (one male and two females) were monitored for at least eight years.

Annual comparisons

Home ranges averaged 201.5 km^2 for resident adult female panthers (n=13, range 81.1-501.8 km^2, sd=101.9), 431.8 km^2 for resident adult male panthers (n=12, range =208.2-752.3 km^2, sd=211.3) , 54.2 km^2 for resident adult female black bears (n=14, range 10.6-205.6 km^2, sd=52.4), 283.7 km^2 for resident adult male black bears (n=15, range 125.5-647.7 km^2, sd=159.8), 14.0 km^2 for resident adult female bobcats (n=4, range 7.0-18.9 km^2, sd=5.3), and 37.5 km^2 for resident adult male bobcats (n=4, range 16.6-66.9 km^2, sd=24.6). Panther home range sizes were comparable to figures reported by Maehr et al. (1991) for the same area, black bear home ranges were larger than those reported for central Florida (Wooding and Hardisky 1988), and bobcat home ranges were nearly identical to those reported for south-central Florida (Wassmer et al. 1988). Measurements of home range size fell within the extremes reported for all three species (Anderson 1983, Hopkins 1989, Wassmer 1988, Carlock et al. 1983, Beck 1991). Statistical comparisons indicated significant differences ($F=13.1$, $p<0.0001$, $df=5$) among annual home range sizes within species/gender groups. However, because black bears exhibit such variable food habits and the diet changes seasonally, this comparison may be misleading if Florida black bears follow the stereotypical pattern of adjusting their movements and home range sizes relative to food availability and denning.

Seasonal Effects

Seasonal comparisons showed that significant differences in home range size among species/gender groups also existed ($F=46.2$, $df=17$, $p<0.0001$). According to this

Table 5.2. Analysis of variance and Duncan's multiple range test results for comparisons of south Florida bobcat, black bear, and panther seasonal home ranges (P=0.05). Means followed by different letters are significantly different from means in the same column.

Species/gender groups	Winter (n)	Summer (n)	Fall (n)	F value	P
Male panthers	319.3 (23)A	329.1 (24)A	330.6 (22) A	0.06	0.942
Female panthers	105.3 (53)B	91.1 (53)B	89.0 (51) BC	1.29	0.277
Male bears	47.2 (29)C	94.4 (19)B	172.2 (24) B	9.32	0.0003
Female bears	5.5 (33)C	15.6 (27)C	36.4 (37)C	11.77	<0.0001
Male bobcats	14.9 (5)C	32.5 (3) BC	9.8 (3)C	2.59	0.136
Female bobcats	9.0 (4)C	7.3 (4)C	5.1 (3)C	0.697	0.526

Table 5.3. Seasonal home range sizes of male and female black bears in southwest Florida, 1991-1994. Means followed by different letters are significantly different from other column means (Duncan's multiple range test, P=0.05).

	Mean home range size (km^2)	
Season	Males	Females
Winter	47.2 A	5.4 A
Summer	94.4 AB	15.6 AB
Fall	172.2 C	36.4 C

analysis, however, male and female black bears were the only groups that exhibited significant seasonal changes in home range size (Table 5.2). For both sexes, black bears had the smallest home range sizes during winter when some individuals were in maternal dens, or in solitary winter dens. Winter ranges were not significantly different from summer ranges, however, because many bears remained active during winter (Table 5.3). Female bears that established natal dens had smaller winter ranges (1.3 km^2, n=8, sd=1.9) than those females that remained active during the winter (13.2 km^2, n=12, sd=8.0)(t=4.1, df=18, p=0.0003) (Table 5.4). Some males also established dens, but most remained active throughout the winter despite utilizing a much reduced area. The mean winter home range size for males that denned was 46.6 km^2 (n=5, sd=30.6), whereas a random sample of males that remained active throughout the winter had a mean home range size of 59.2 km^2 (n=10, sd=50.2). Males with winter dens had smaller home ranges than those without them, but this difference was not significant (t=0.51, p=0.62, df=13). Although males such as M08 built elaborate ground nests out of matted saw grass and swamp ferns, or, like M20, inhabited small areas within isolated saw palmetto thickets, movement data as well as signs of feeding on herbaceous matter and fresh feces at the edges of these dens indicated that denning males occasionally left their winter refugia to feed. If the foods available to black bears during winter were of sufficient quality to maintain body mass as was indicated for several south Florida plant species (see dietary overlap chapter), this would help to explain winter activity and the more rapid growth rates of Florida black bears versus black bears in more northern latitudes or in colder climates (see Appendix B). What is inexplicable is the absence of movements among denning females despite warm

Table 5.4. Winter home range sizes of adult female black bears in southwest Florida, 1992-1994.

		Home range size (km^2)	
Bear ID#	Year	With natal den	Without natal den
F02	1992	0.9	
F02	1993		20.8
F03	1993	0.03	
F03	1994		8.3
F05	1992		27.7
F05	1993		12.8
F05	1994	1.3	
F06	1992		2.4
F06	1993	0.5	
F07	1992		15.8
F08	1992	1.0	
F08	1993	5.9	
F09	1992	0.5	
F09	1993		2.6
F10	1993		8.0
F12	1994		20.2
F13	1993	0.2	
F13	1994		7.9
F17	1993		11.0
F19	1993		21.3
	Mean	1.3 (sd=1.9)	13.2 (sd=8.0)

temperatures and the availability of foods, some of which are highly digestible (palm heart fibers) and high in fat content (Brazilian pepper seeds). Apparently, the evolutionary roots of the black bear's reproductive cycle that may date to a cold Pleistocene climate are sufficiently strong to have prevented winter activity among denning females, even though an energetic advantage may be obtained from occasional winter feeding. Nonetheless, home range shifts caused by food availability changes, reproductive behavior, and possibly, hibernation, suggested that season must be taken into account when comparing home ranges of sympatric carnivores in south Florida.

Male panthers exhibited larger home ranges in every season than any other species/gender groups (Table 5.2). During winter, female panthers had larger home ranges than black bears and bobcats, which were not significantly different from each other. In summer, home ranges of female panthers, male black bears, and male bobcats were not distinguishable from each other, but female panther and male black bear home ranges were larger than home ranges of female black bears and female bobcats. The home range sizes of the latter two species/gender groups were indistinguishable from those of male bobcats. During fall, male black bear home ranges were larger than those of female black bears and bobcats, but were not distinguishable from female panther home range sizes. In general, home range dynamics in black bears explains the seasonal variation in home range size differences among all three large south Florida carnivores.

Home range size relationships remained constant between male and female panthers, likely due to prey distributions that did not change seasonally (Land et al. 1993), and due to the nearly continuous constraints placed on female panther movements by their

kittens (Maehr et al. 1989a, 1991). Maehr et al. (1991) found that non-reproductive but otherwise healthy adult female panther #18 exhibited a home range that was comparable in size to some resident males. In contrast, although bobcats did not exhibit significant seasonal changes in home range size, they differed from both black bears and panthers in that there were no gender-related differences in home range size during any season (Table 5.2). Anderson (1987) indicated that bobcats exhibit pronounced sexual dimorphism, however, bobcat mass measurements in this study (Table 5.1) suggested that such differences were slight. Mass measurements in Foster (1992) indicate that males were 27% larger than females in the same study area ($t=9.5$, $p<0.0001$, $df=16$), a difference which is at the low end of the spectrum for sex-related mass differences in this species. Relatively similar body sizes may help to explain similar patterns in use of the landscape, particularly as would result from male and female bobcats utilizing similar habitat and prey resources. It is of interest that the only season where bobcat home range size approached significance over smaller means was for males during summer (Table 5.2). This season overlaps with periods of female fertility in other areas (Crowe 1975, Mehrer 1975), thus larger home ranges may have resulted from increased movements of males in search of mates. Unfortunately, there is insufficient information on bobcat reproductive characteristics (Anderson 1987), and even less on bobcat reproduction in Florida, to rule out other factors that may explain this pattern such as variation in food resources.

Because of its tropical influence, low latitude, and its limited altitudinal variation, seasonal effects such as daylength and temperature are dampened or moderated in south Florida. Further, a high level of habitat interspersion provide year-round food resources

for herbivorous prey species. Land et al. (1993) found that white-tailed deer in southwest Florida responded to changes in food availability but did not exhibit disjunct use areas. The abandonment by some western ungulates of summer ranges compels sympatric cougars to display altitudinal home range dynamics (Rasmussen 1941, Seidensticker et al. 1973). Florida panthers can maintain consistent use of home ranges because prey densities remain relatively constant throughout the year (Figs.5.1-5.13). Some changes in the distribution of radio location frequency within home ranges of female panthers can be attributed to denning and kitten rearing (Maehr et al. 1989a)(Figs. 5.1,5.2,5.3,5.4,5.8). In the case of adult male #13, his southward shift and home range contraction in 1987 (Fig. 5.7) was in response to early maturing female panther kittens, and possibly, attempts to avoid the resident adult males in the area (Maehr et al. 1989a, 1991).

Rodents and lagomorphs maintain small areas of activity throughout the year (see Holler 1992, Chapman et al. 1982) and do not appear to shift home ranges seasonally. Further, in Florida most bobcat prey species remain active year-round and provide bobcats with geographically stable food supplies. Bobcats in southwest Florida exhibited the consistent annual home range patterns (Figs. 5.14 and 5.15) predicted by a constant food supply and common to other studies of the species in the southeast (Wassmer et al. 1988). Only during winter is there a potential for measurable and predictable changes in food availability as avian migrants such as gray catbirds descend upon south Florida's forests. Maehr and Brady (1986) measured an increase in bird consumption by Florida bobcats that coincided with the peak in land bird abundance in this part of the state (Robertson and Kushlan 1974). Distribution of these temporary residents is temporally unpredictable or spatially even enough so that the landscape-level responses in home range use exhibited by

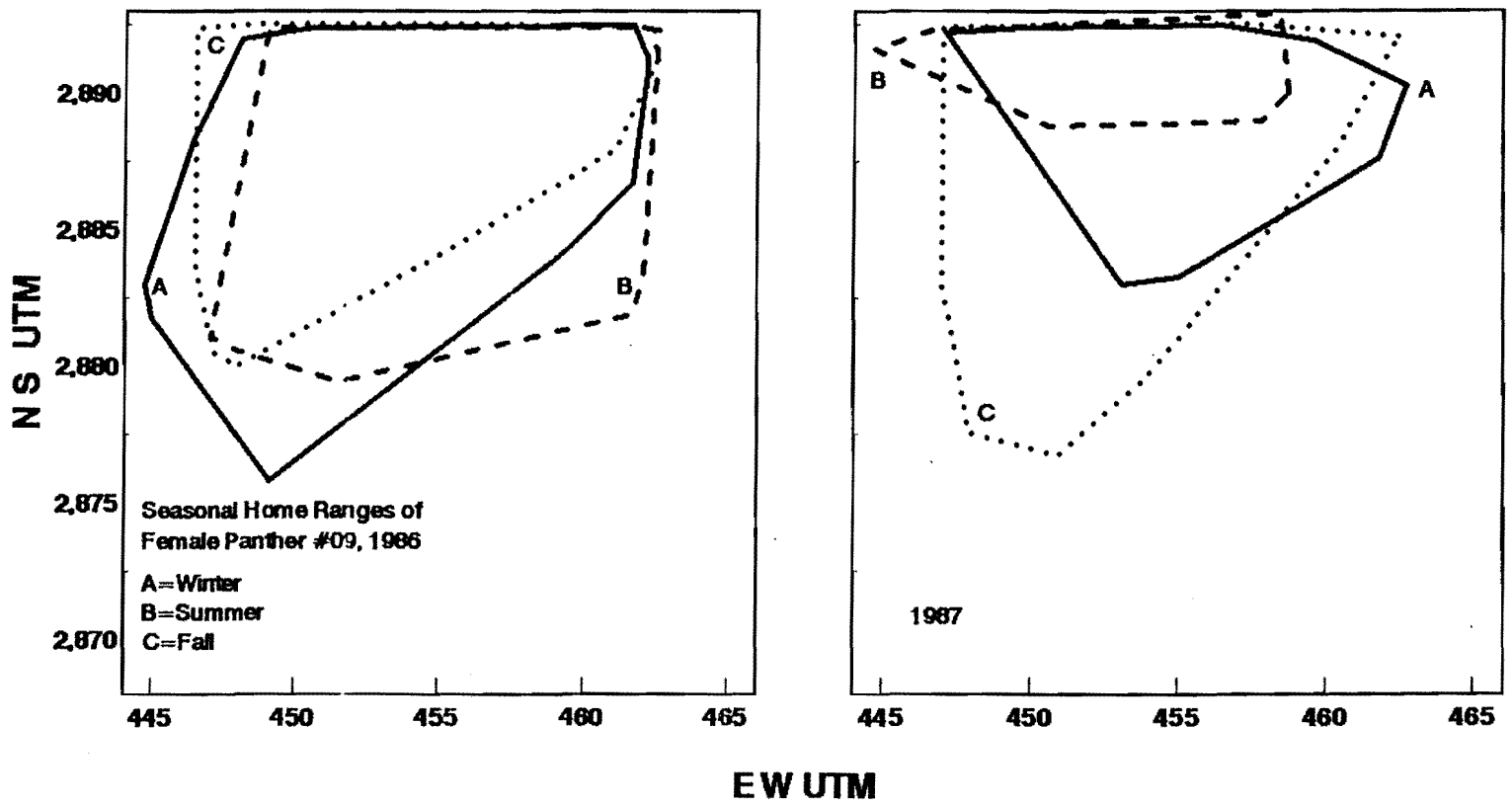


Figure 5.1. Seasonal home ranges of female panther #09 during 1986 and 1987.

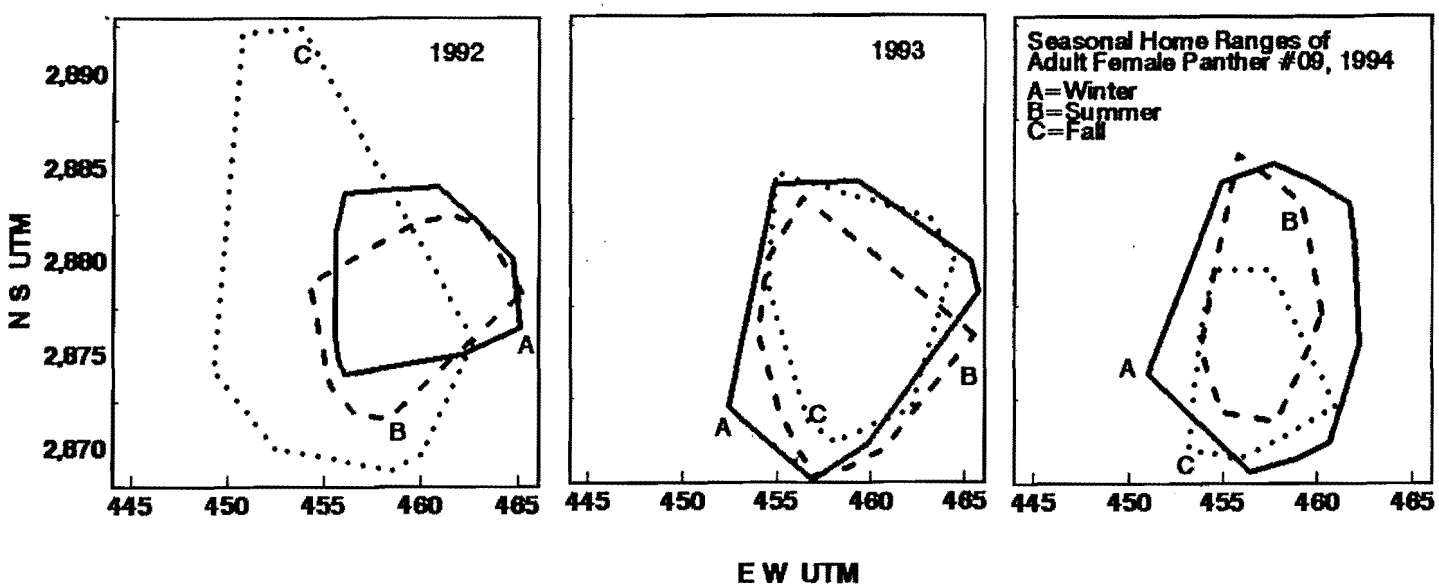


Figure 5.2. Seasonal home ranges of female panther #09 during 1992, 1993, and 1994.

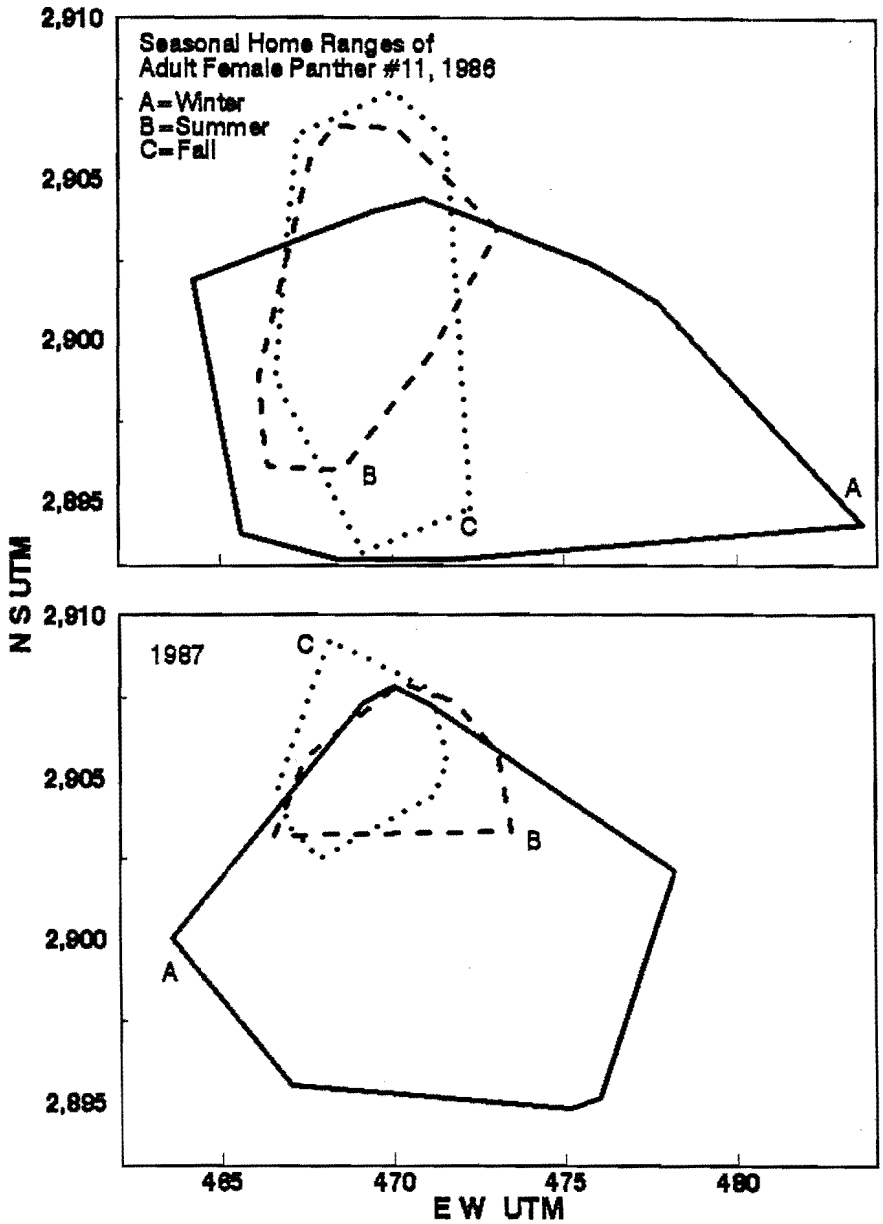


Figure 5.3. Seasonal home ranges of female panther #11 during 1986 and 1987.

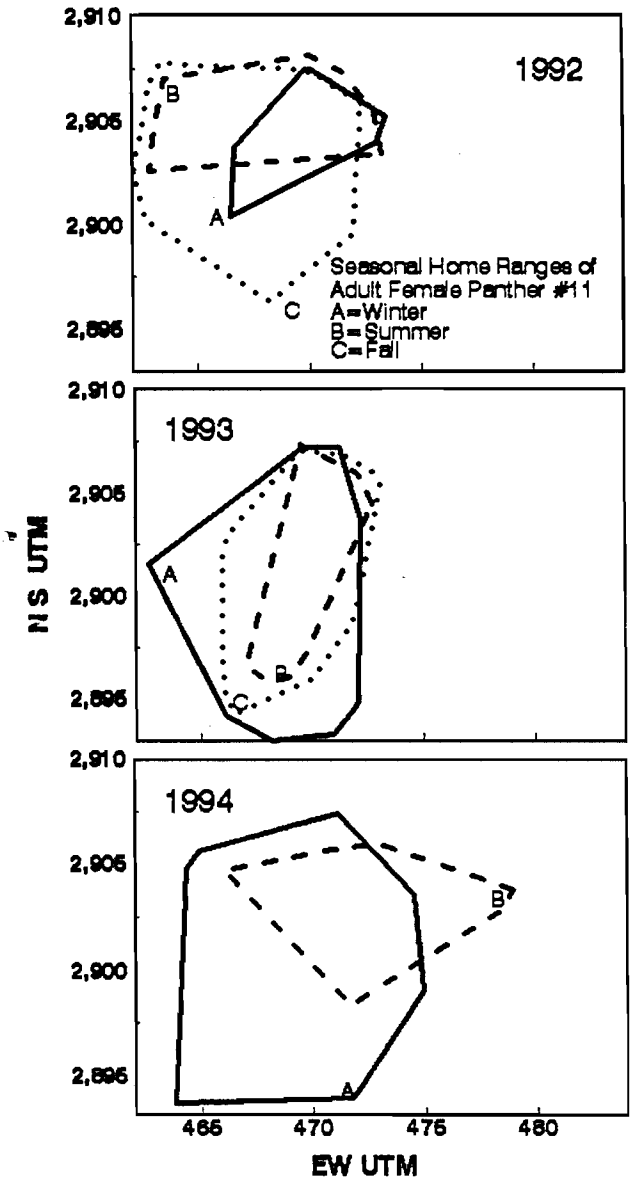


Figure 5.4. Seasonal home ranges of female panther #11 during 1992, 1993, and 1994.

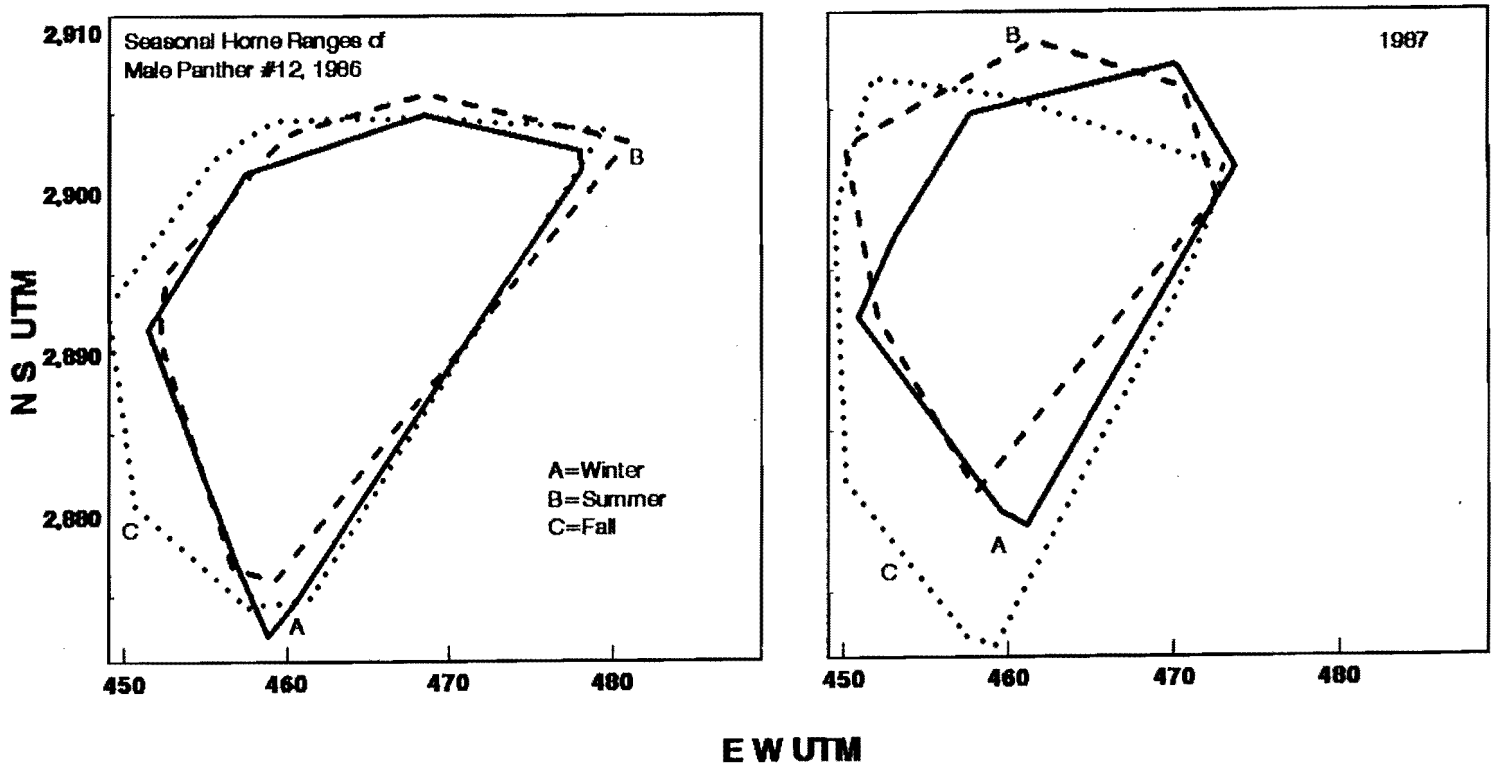


Figure 5.5. Seasonal home ranges of male panther #12 during 1986 and 1987.

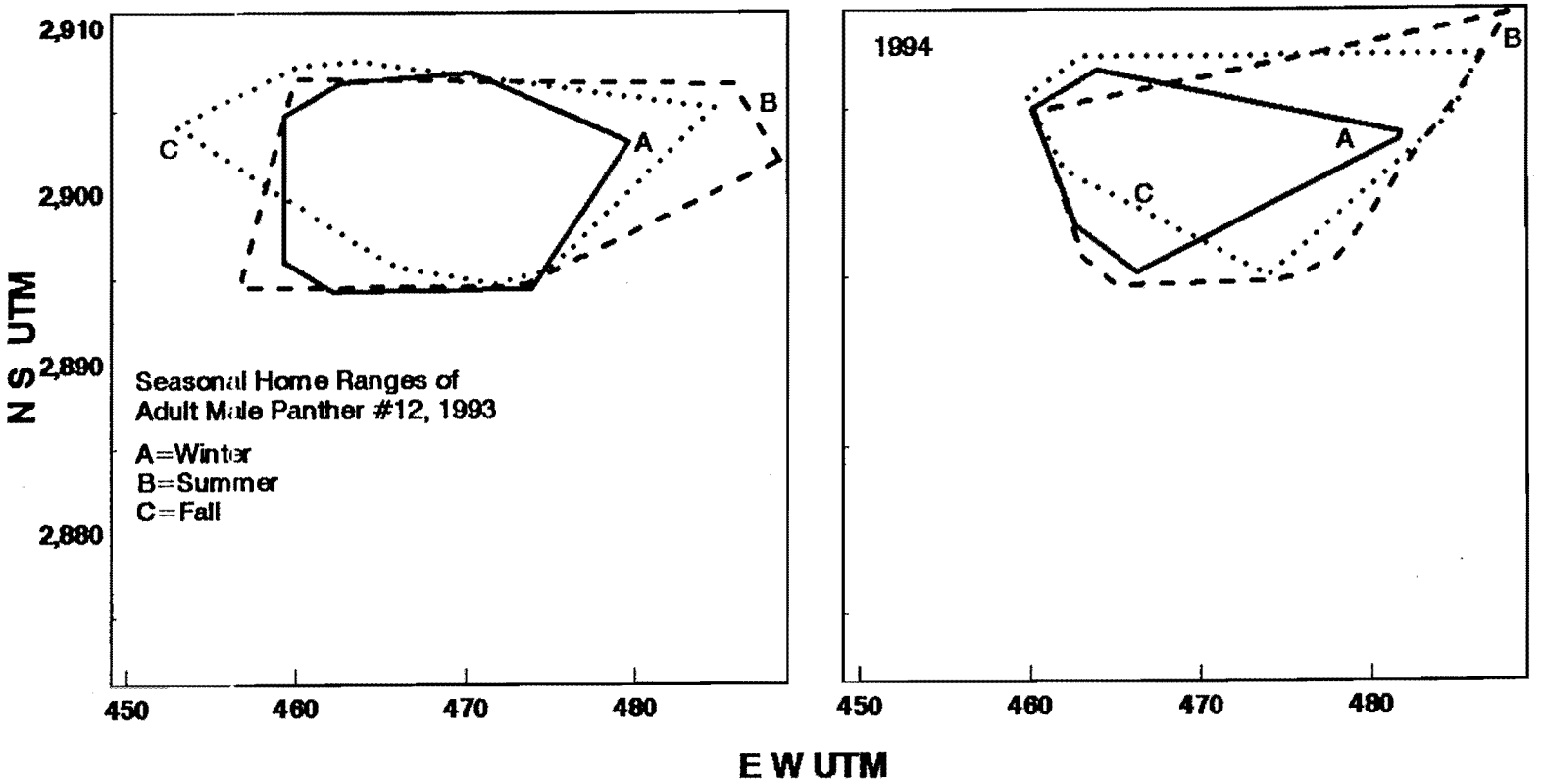


Figure 5.6. Seasonal home ranges of male panther #12 during 1993 and 1994.

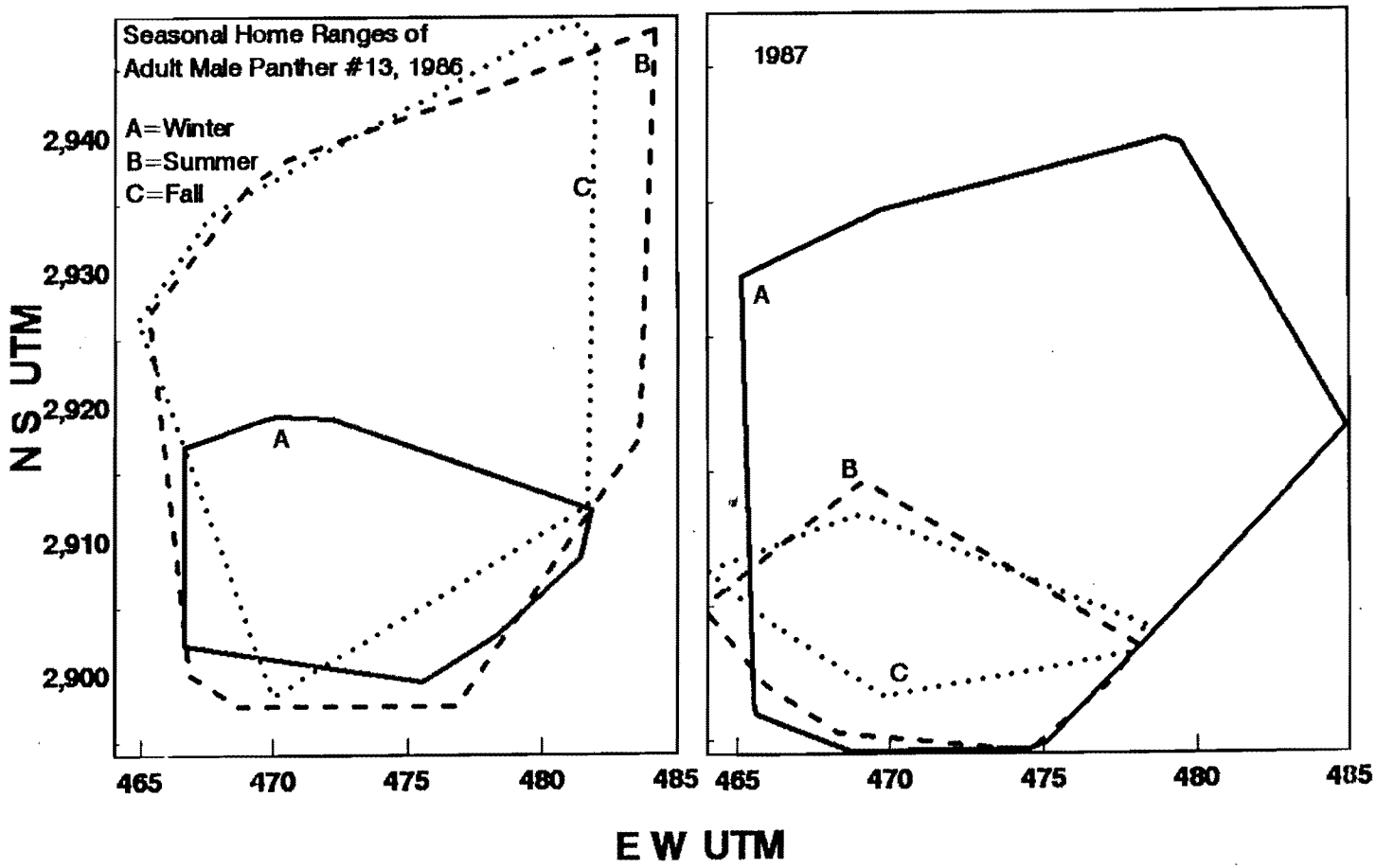


Figure 5.7. Seasonal home ranges of male panther #13 during 1986 and 1987.

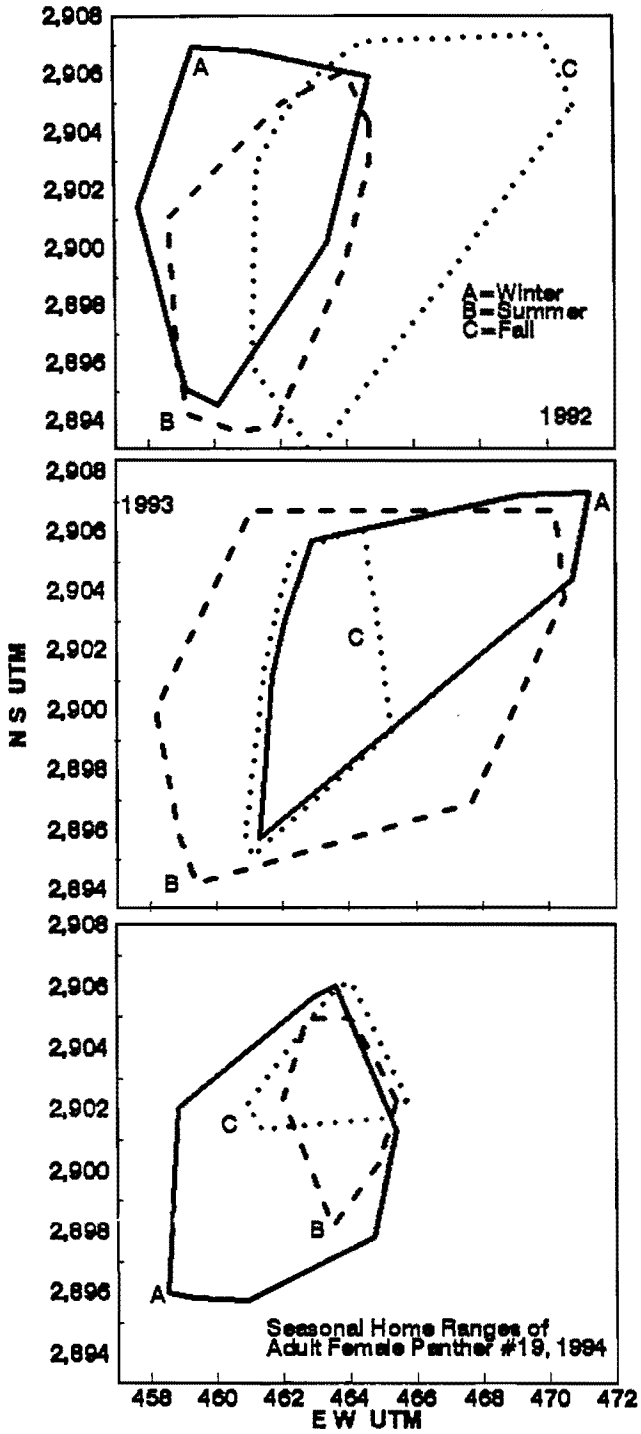


Figure 5.8. Seasonal home ranges of female panther #19 during 1992, 1993, and 1994.

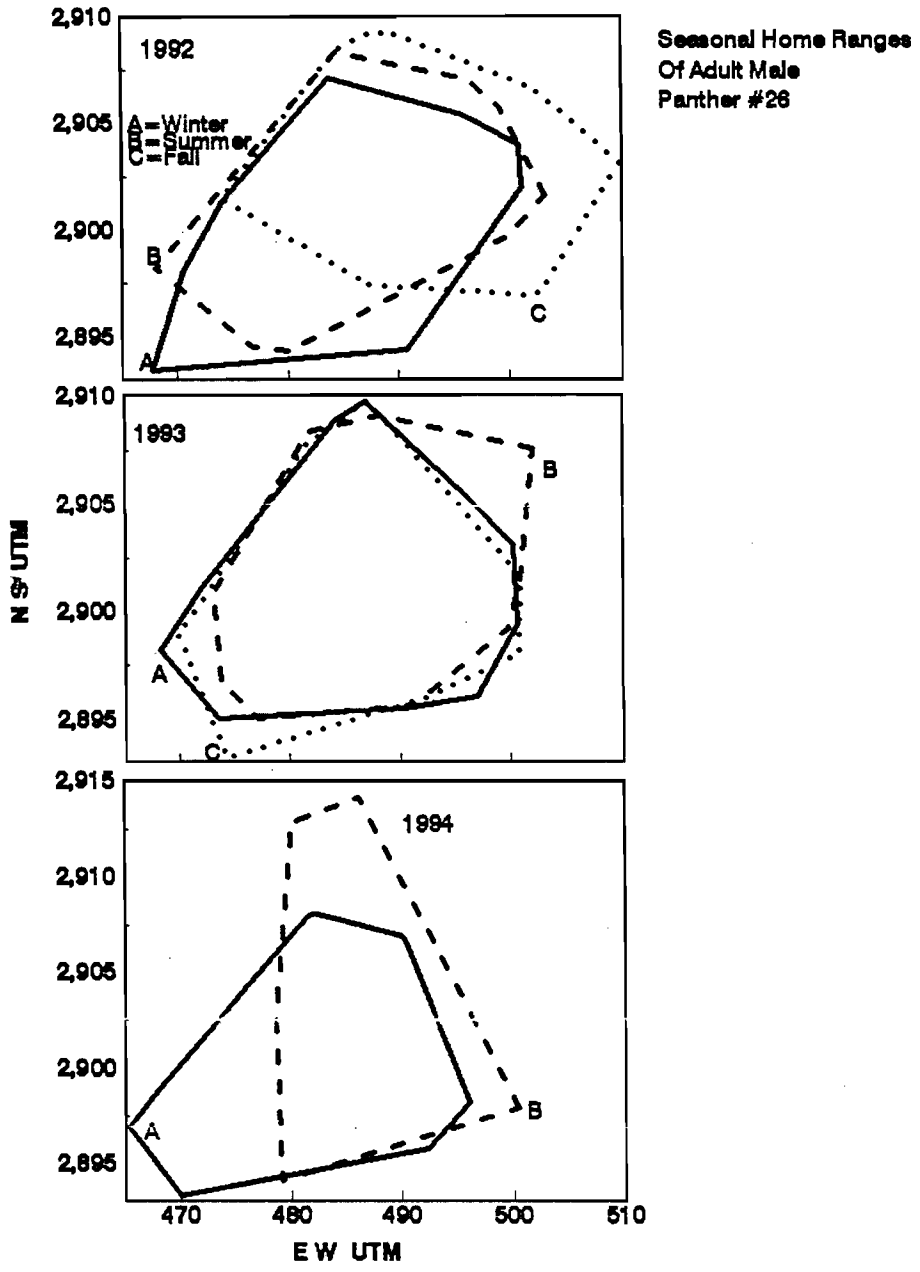


Figure 5.9. Seasonal home ranges of male panther #26 during 1992, 1993, and 1994.

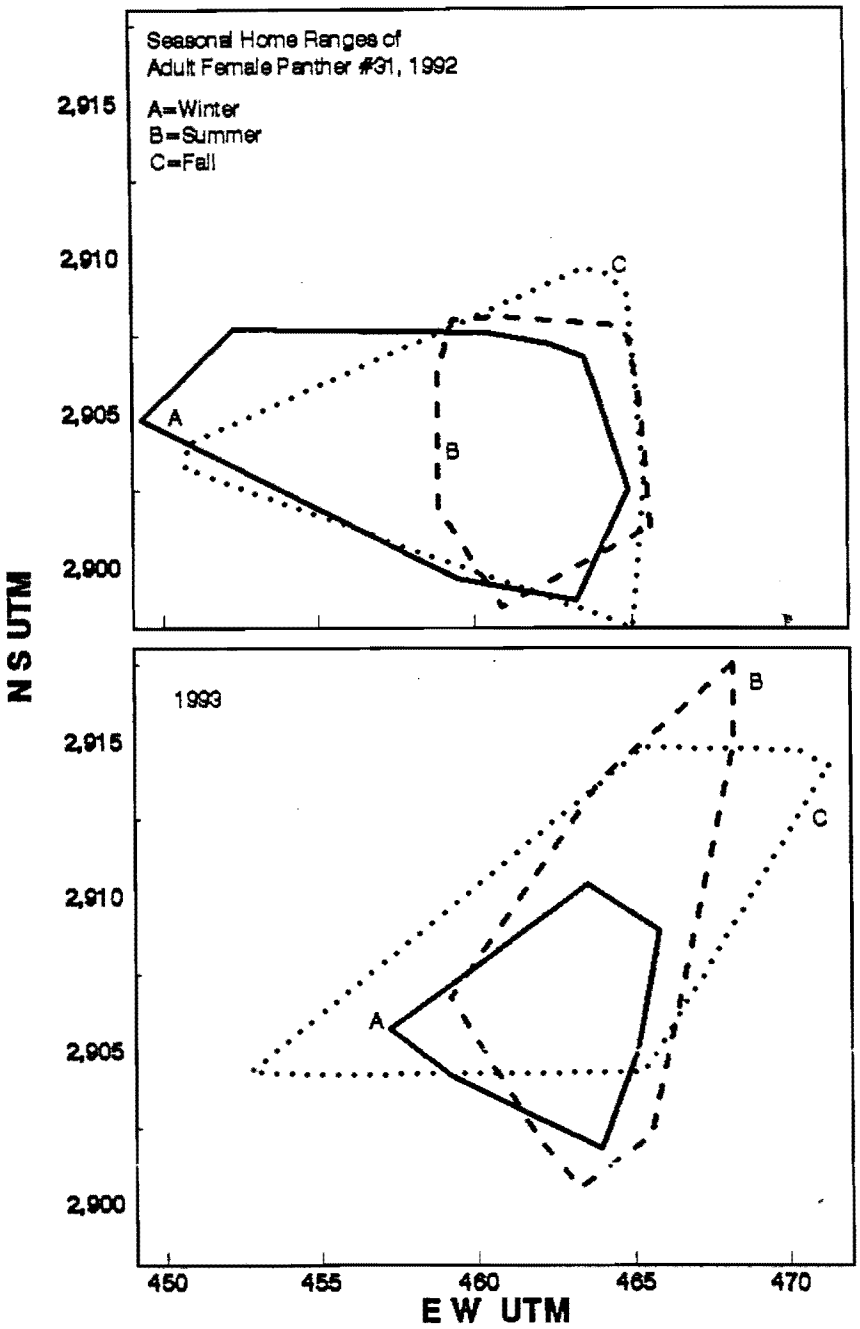


Figure 5.10. Seasonal home ranges of female panther #31 during 1992 and 1993.

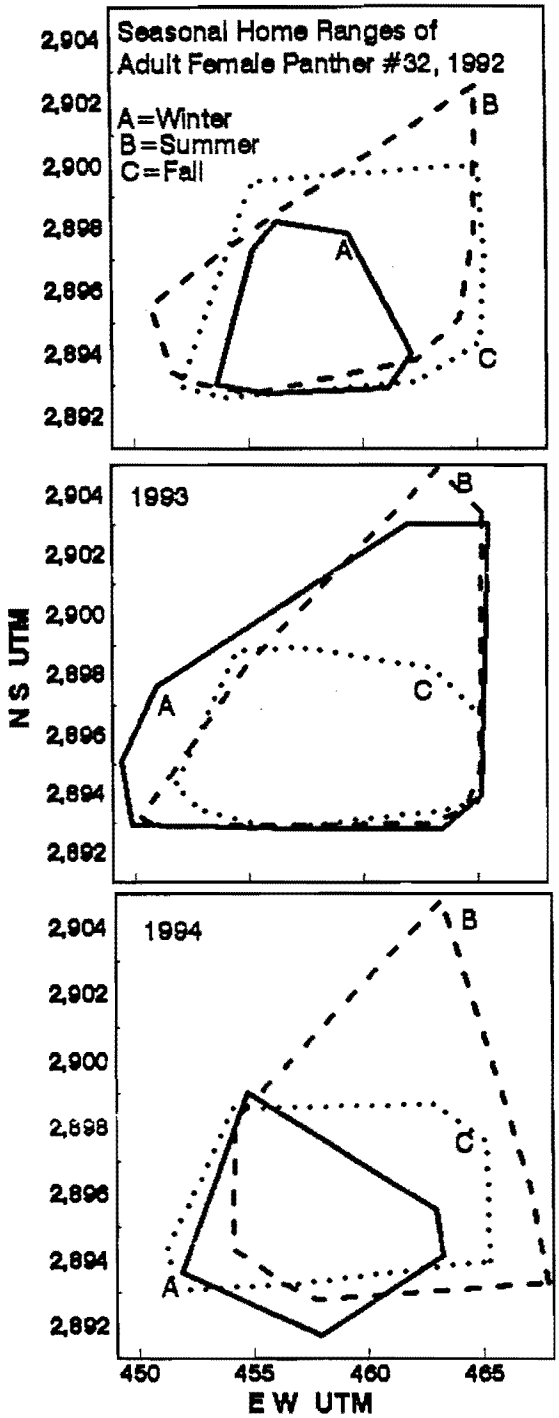


Figure 5.11. Seasonal home ranges of female panther #32 during 1992, 1993, and 1994.

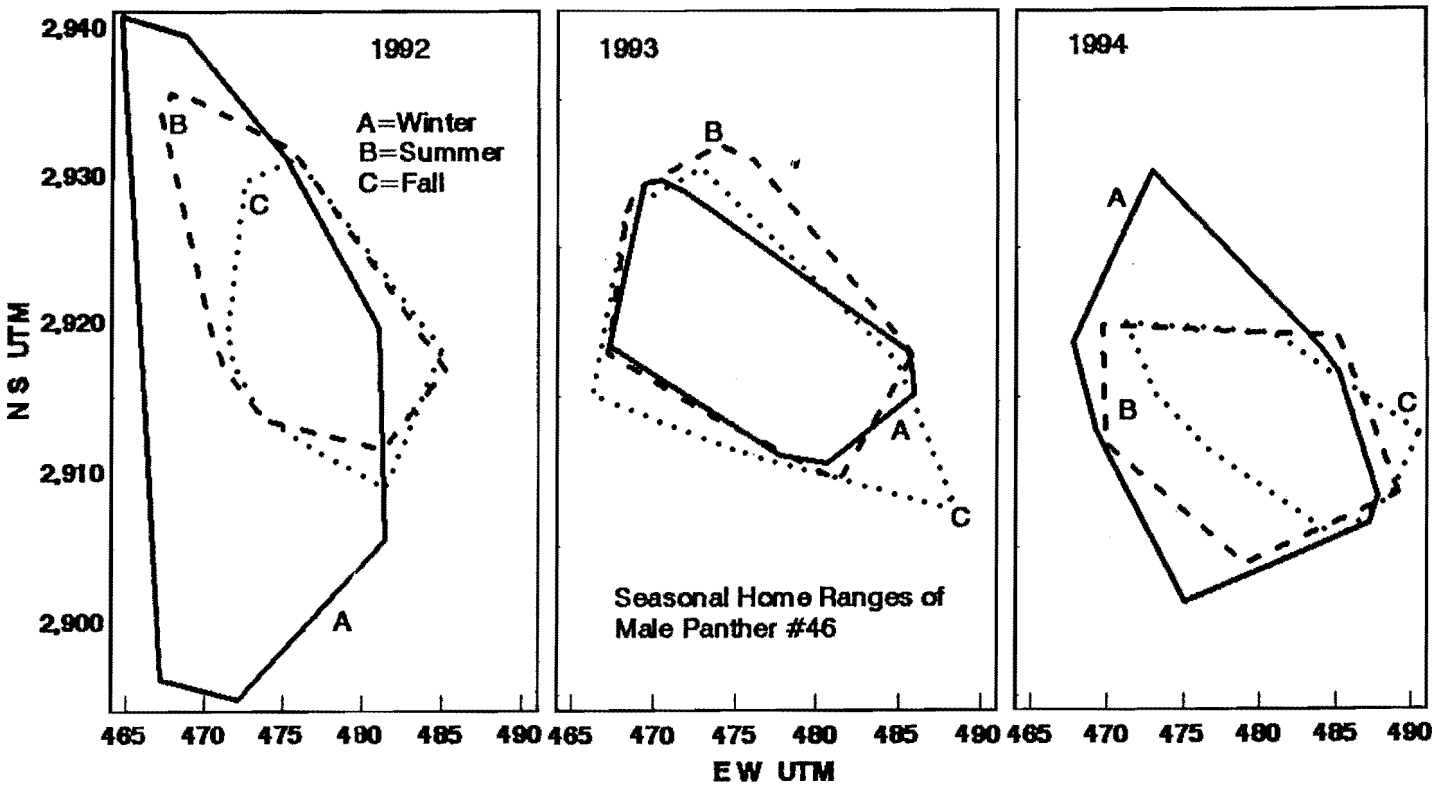


Figure 5.12. Seasonal home ranges of male panther #46 during 1992, 1993, and 1994.

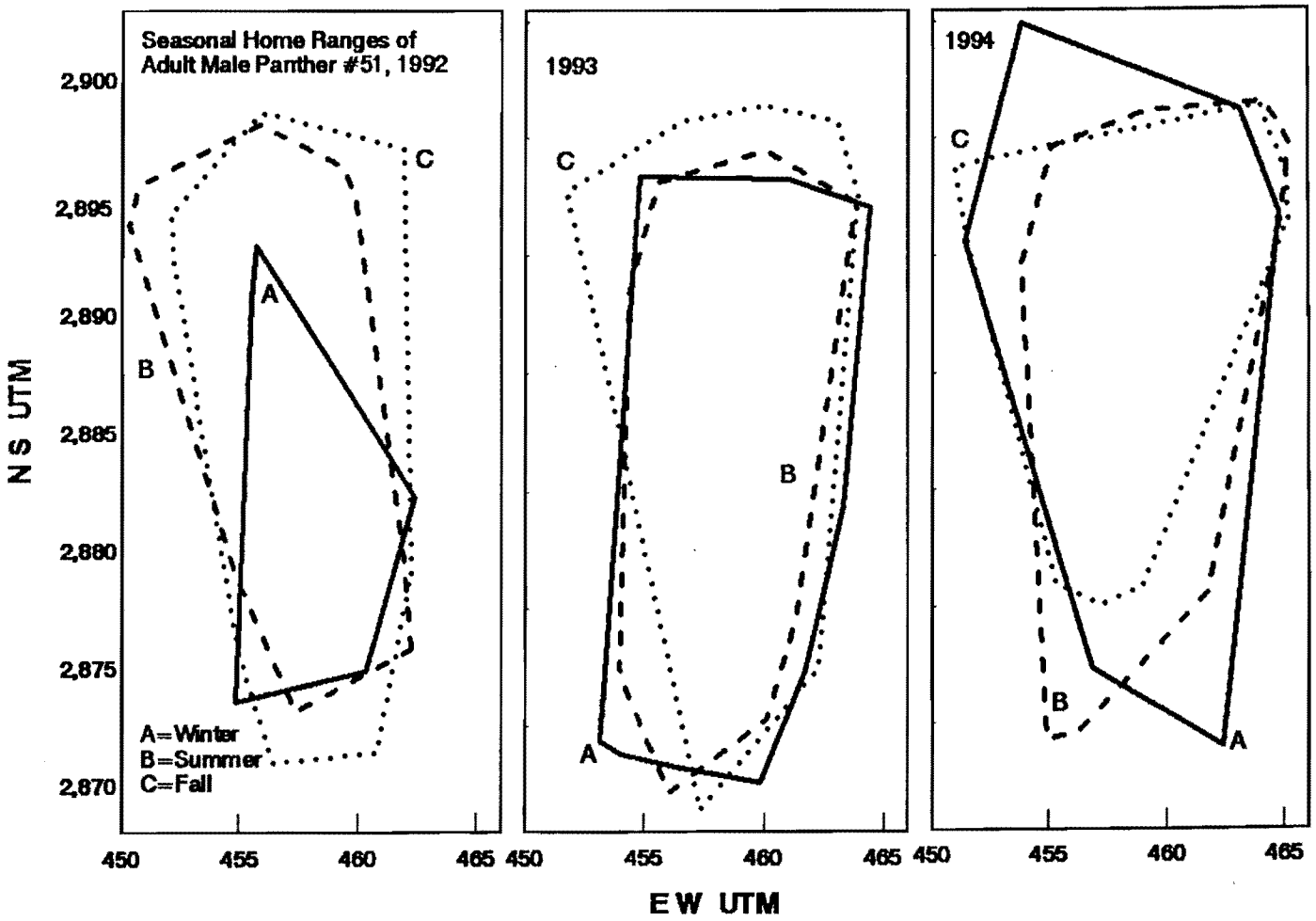


Figure 5.13. Seasonal home ranges of male panther #51 during 1992, 1993, and 1994.

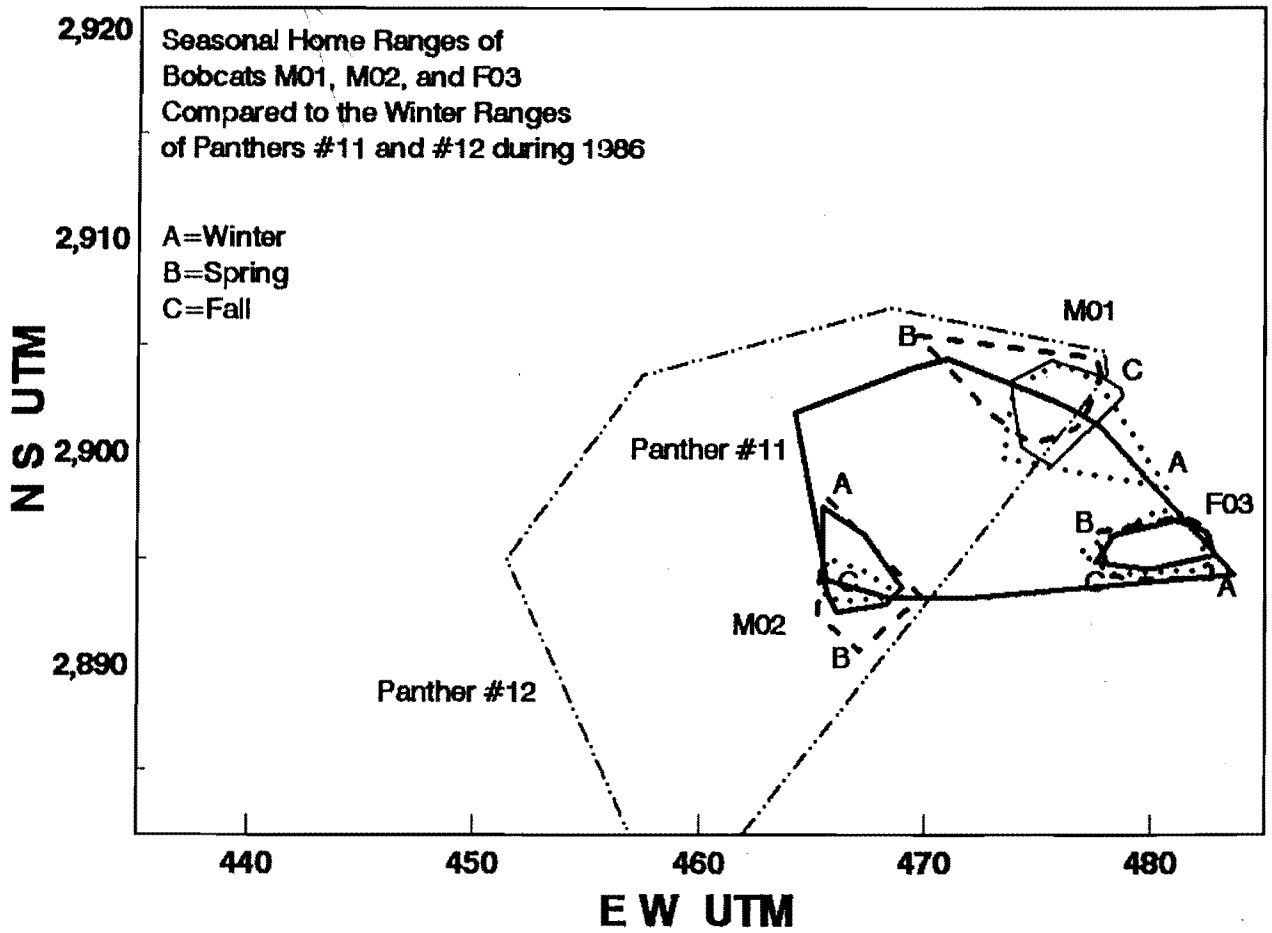


Figure 5.14. Seasonal home ranges of three bobcats compared to the winter range of female panther #11 and male panther #12 during 1986.

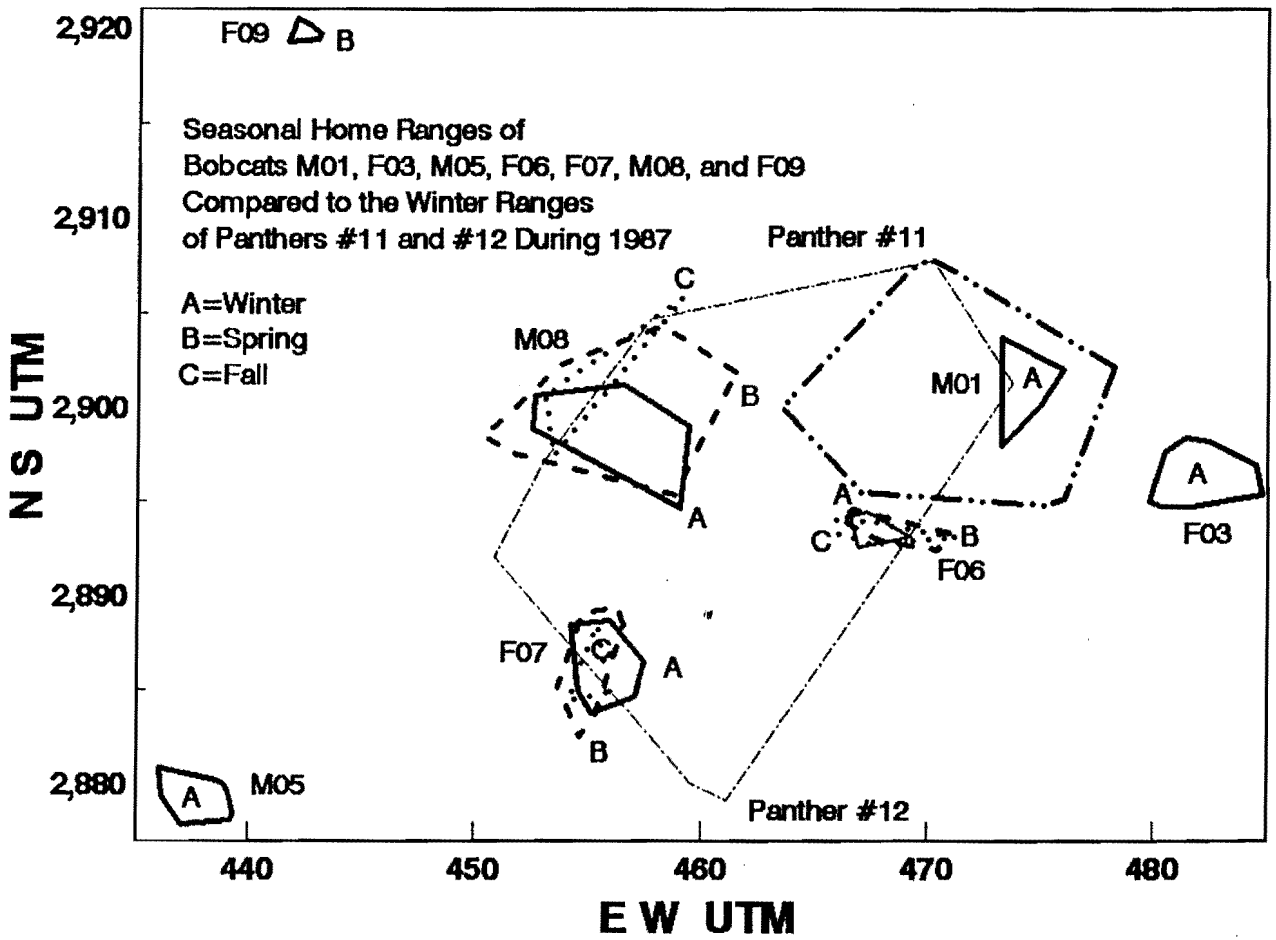


Figure 5.15. Seasonal home ranges of seven bobcats compared to the winter range of female panther #11 and male panther #12 during 1987.

black bears to clumped and ephemeral food supplies does not occur; bobcats apparently utilize such prey as they become available without making home range shifts. If bobcats alter their prey search images during such times of superabundant avian prey, then as Maehr and Brady (1986) found, migrants as well as resident, over-wintering breeders should be expected to increase in bobcat diets as well. With the return of neotropical migrants to northern breeding grounds, the diets of south Florida bobcats return to a predominantly rodent and lagomorph fare without causing significant effects on home range size.

Black bears in south Florida follow patterns of home range dynamics that are generally similar to those of the species throughout its range (Figs. 5.16-5.24). For both males and females, home range size was smallest during winter, however, the amount of variation among individuals during this time of year made differences between summer home range sizes insignificant (Table 5.3). Fall black bear home ranges of males and females were significantly larger than those of other seasons.

Among all sex and age classes, only pregnant black bears consistently ceased movements during winter and denned. Den entrance and emergence dates averaged 29 January and 18 April, respectively. Sizes of neonates handled in dens suggested that parturition in south Florida black bears occurs on about 1 March. Four adult females are known to have abandoned den sites. F04, and F11 abandoned dens in open wetland settings after their solitary cubs were handled by researchers in 1992 and 1993, respectively. F07 apparently abandoned a site located in a mangrove swamp after an unusually high tide and unusually high rainfall inundated her den during March 1993. F17

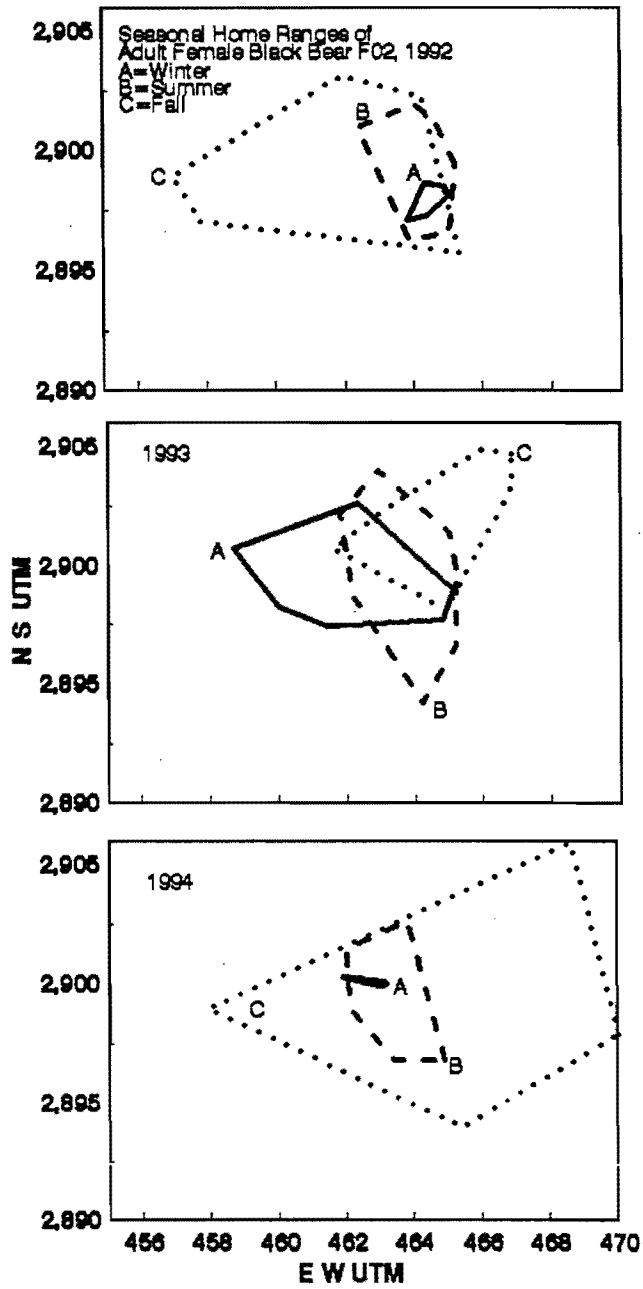


Figure 5.16. Seasonal home ranges of female black bear F02 during 1992, 1993, and 1994.

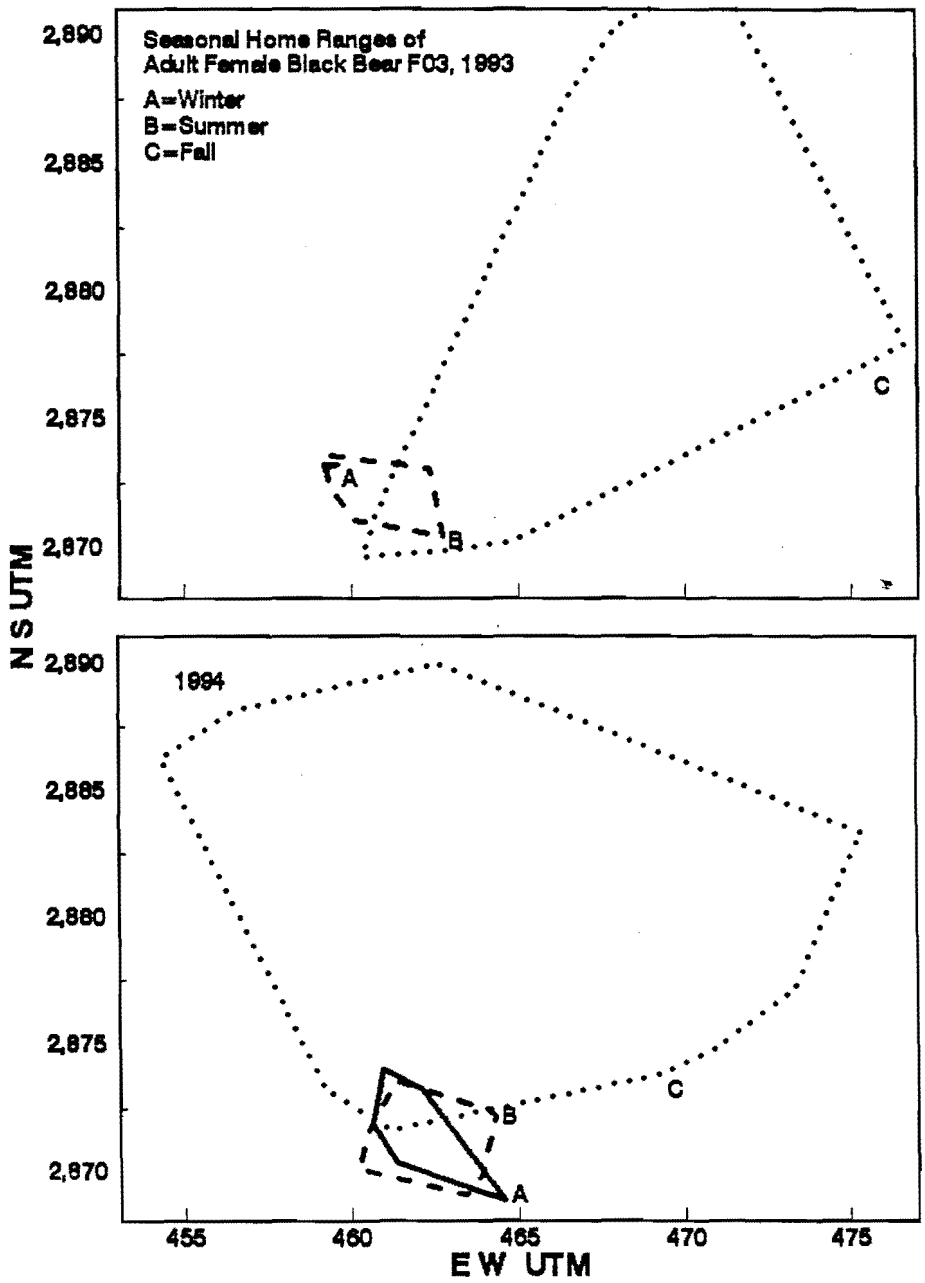


Figure 5.17. Seasonal home ranges of female black bear F03 during 1993 and 1994.

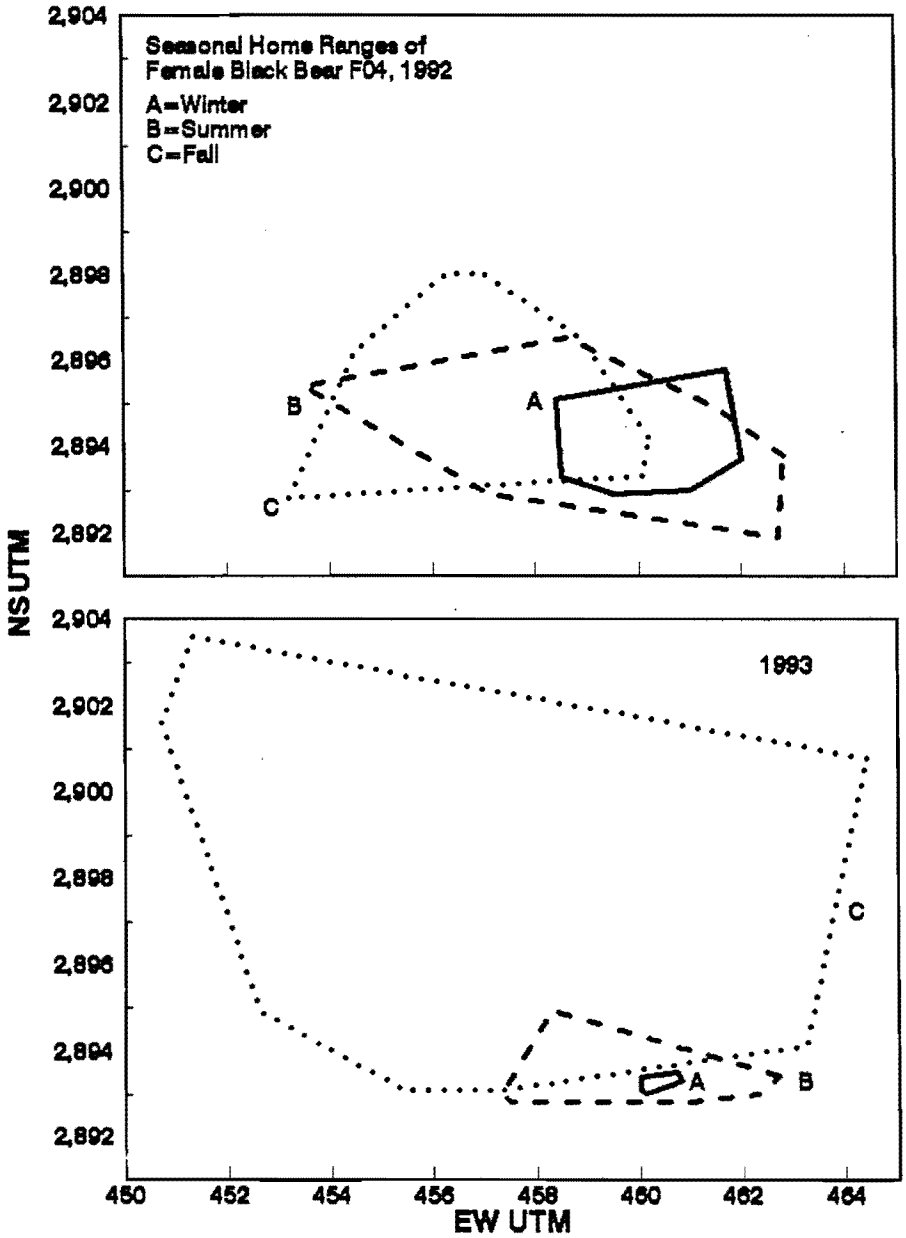


Figure 5.18. Seasonal home ranges of female black bear F04 during 1992 and 1993.

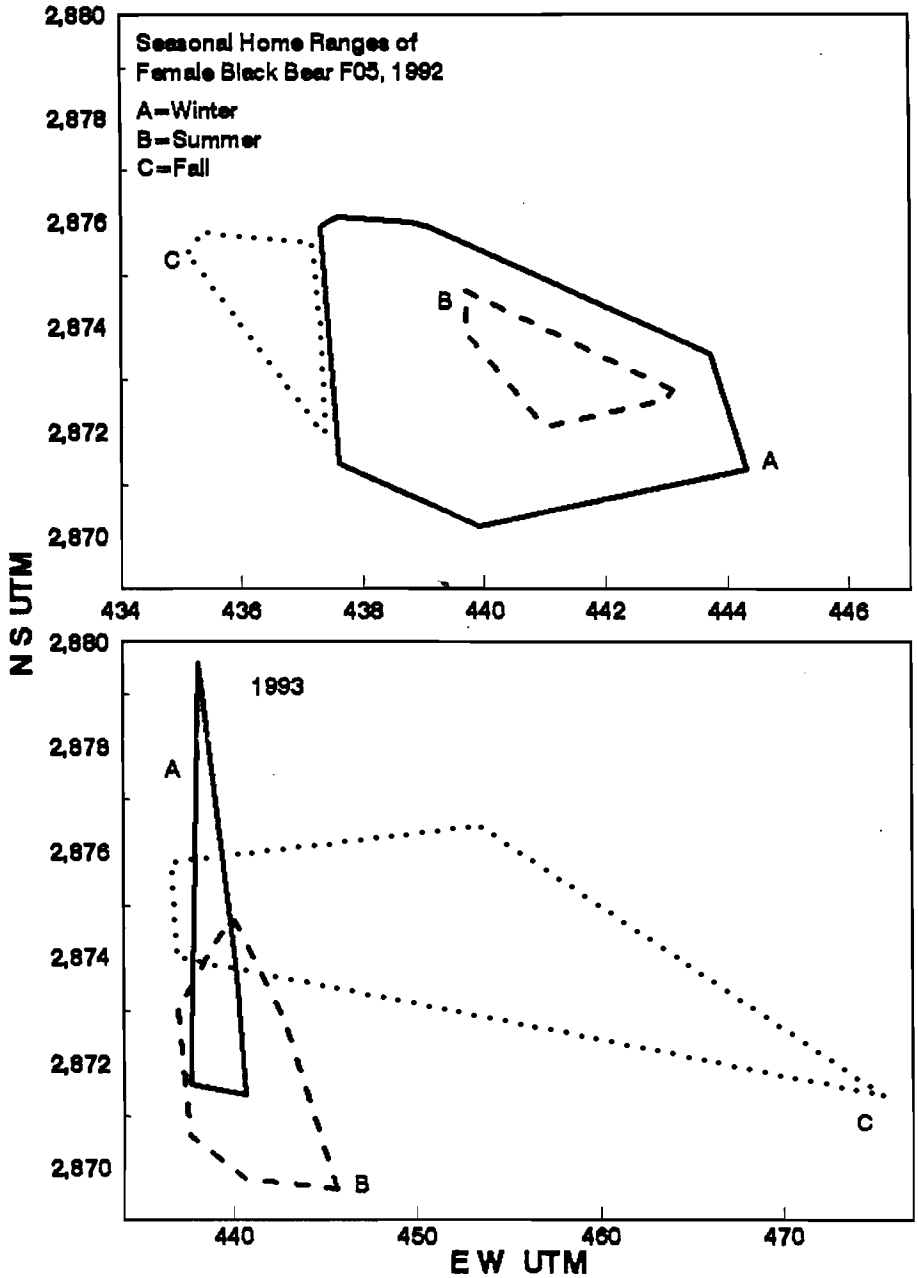


Figure 5.19. Seasonal home ranges of female black bear F05 during 1992 and 1993.

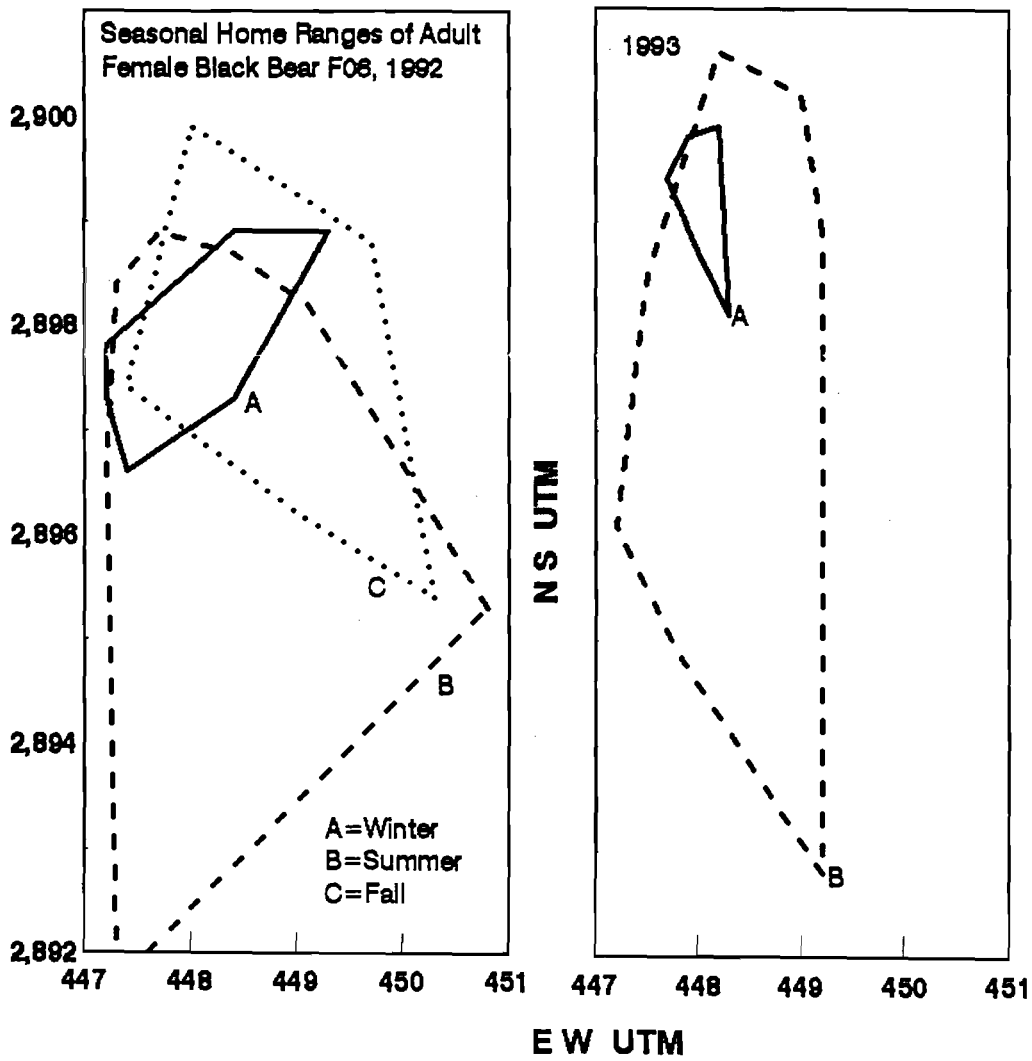


Figure 5.20. Seasonal home ranges of female black bear F06 during 1992 and 1993.

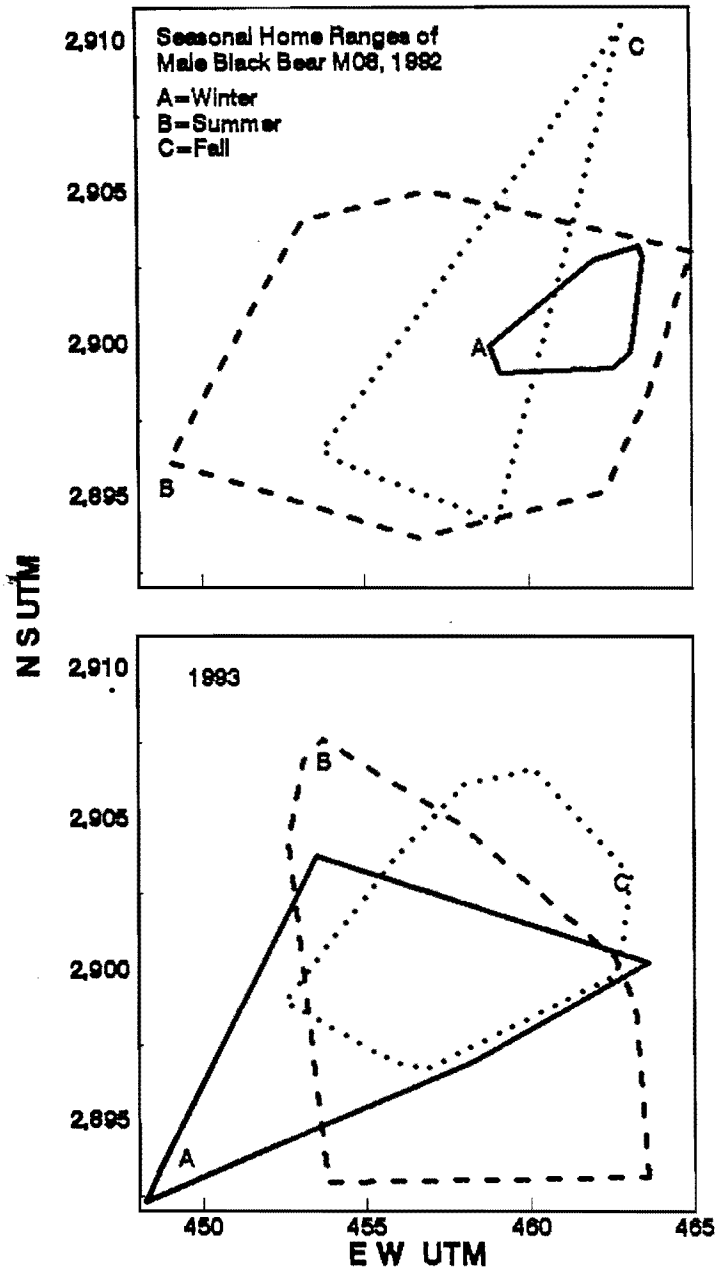


Figure 5.21. Seasonal home ranges of male black bear M08 during 1992 and 1993.

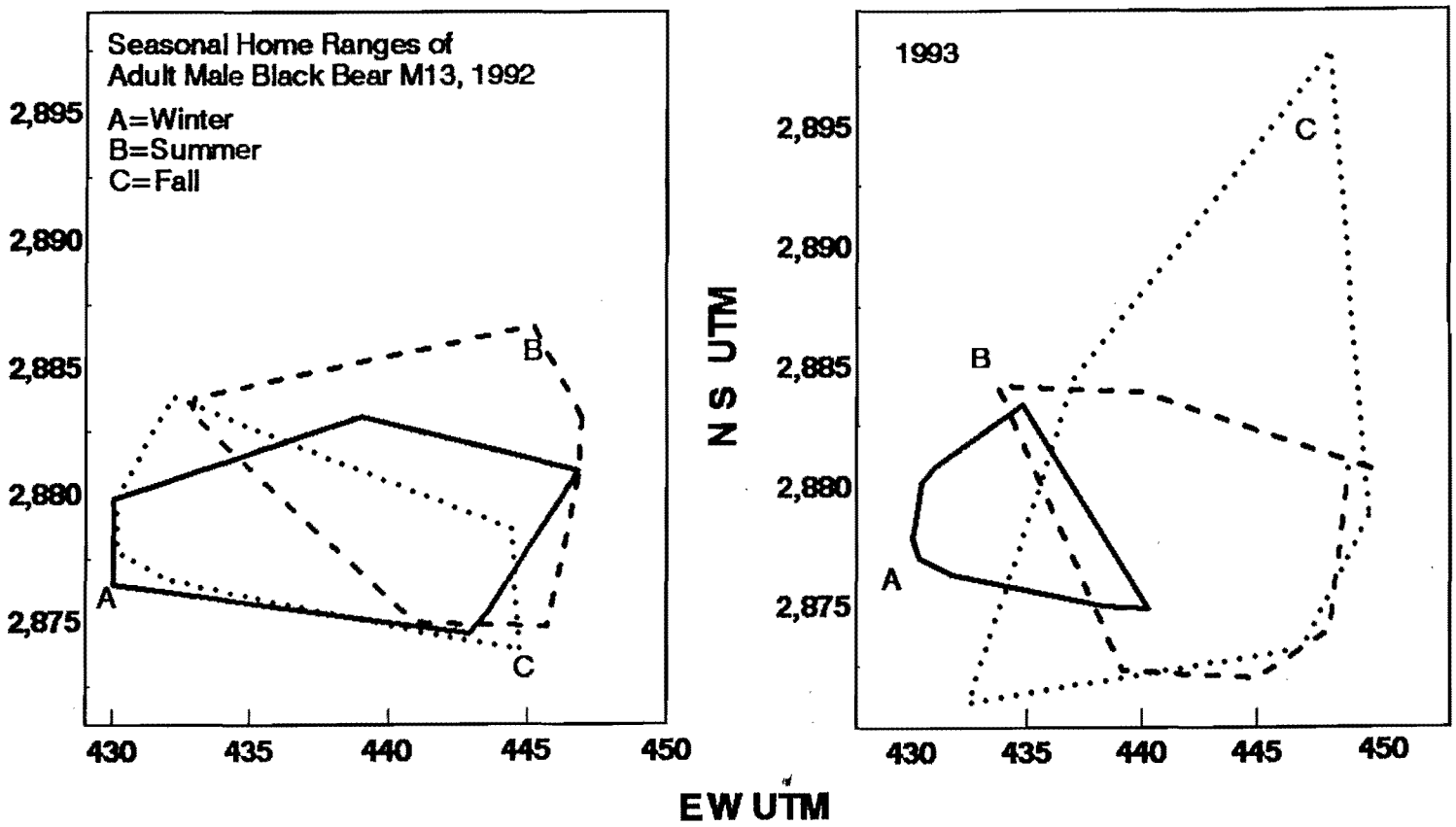


Figure 5.22. Seasonal home ranges of male black bear M13 during 1992 and 1993.

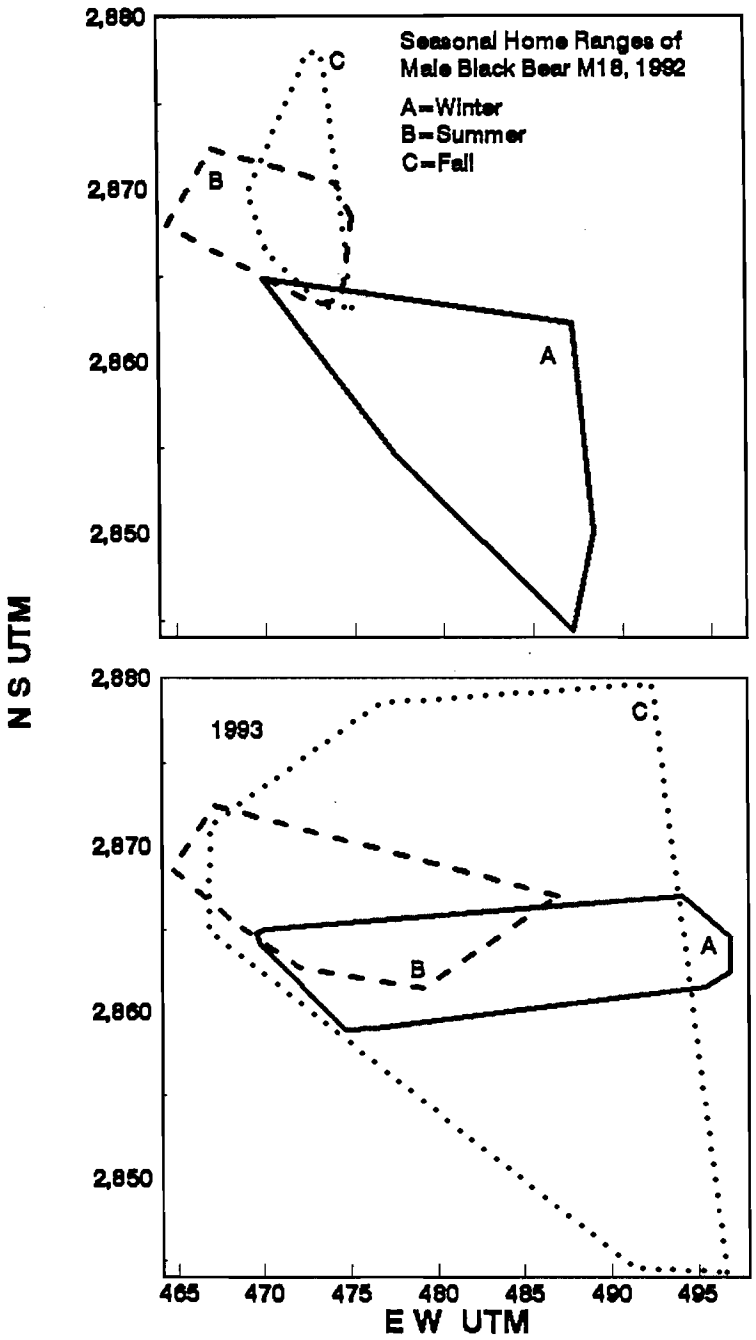


Figure 5.23. Seasonal home ranges of male black bear M18 during 1992 and 1993.

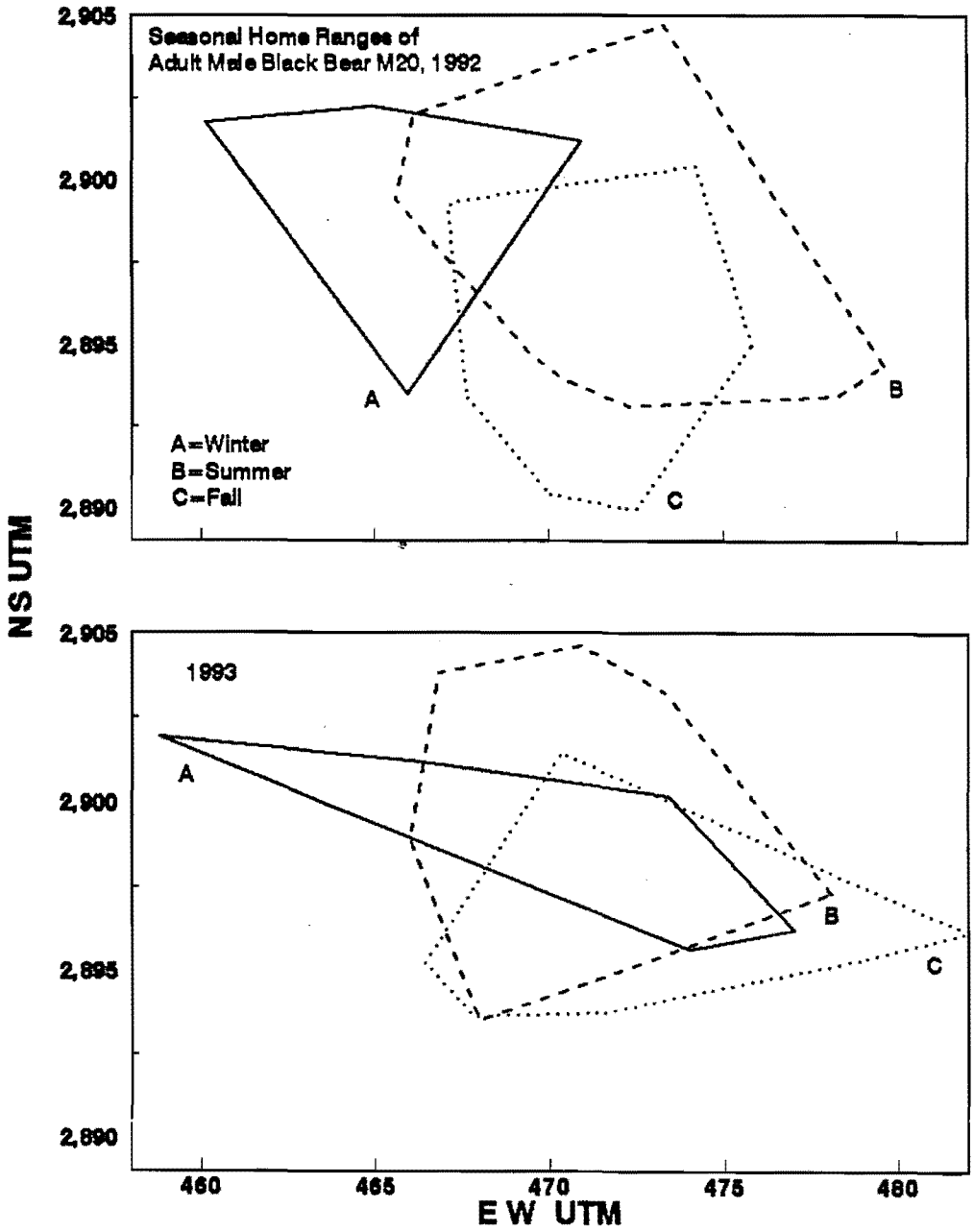


Figure 5.24. Seasonal home ranges of male black bear M20 during 1992 and 1993.

abandoned a natal den after the saw palmetto thicket in which it was located was burned by a prescribed fire on the Florida Panther National Wildlife Refuge on 28 February 1994.

Solitary adult females, and adult females with dependent cubs from the previous year remained active during winter. The exception to this pattern was an adult female with three nine-month old cubs that was hit by a car sustaining a broken humerus, and broken mandible on 12 December 1993. After F21 was taken 100 m from the highway, she remained stationary for the remainder of the winter in a hardwood hammock. The three cubs were seen periodically after the accident feeding on live oak acorns and are presumed to have survived. F21 made small movements around this site until 6 April 1994 when she resumed normal movement patterns that were indistinguishable from other female black bears (Fig. 5.25). Comparable healing abilities were observed in an adult female black bear in Ocala National Forest in 1985 (Maehr pers. observ.). After breaking the ulna and radius in a snare, the bear was recaptured 30 days later in a culvert trap with both bones fully healed and exhibiting a weight gain of 6.8 kg. Black bears throughout their range tolerate a wide range of injuries to limbs (i.e. Stone et al. 1975, Anderson 1989) that would likely be fatal to wild felids.

Some adult males maintained winter dens, but denning bouts were occasionally interrupted by short movements away from the den. Average den entrance and emergence dates for male black bears were 10 February and 24 March, respectively, and did not appear to be age-related (n=8, range of 2-10 years of age). Duration of den attendance by male black bears ranged from 13 to 50 days and averaged 33.3 days (n=9, sd=12.1). Male

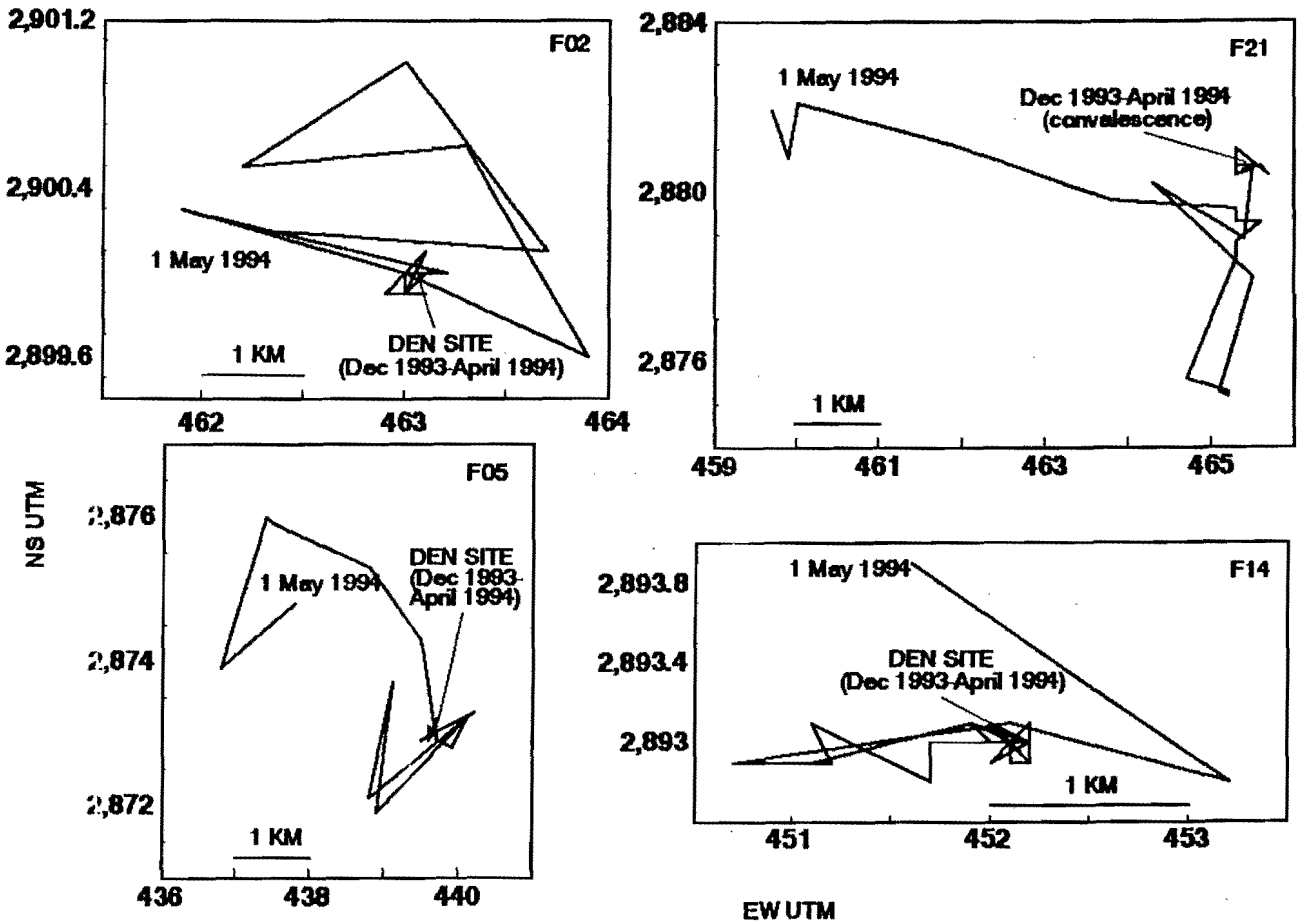


Figure 5.25. Comparison of winter home ranges between injured female black bear F21 and three female black bears with cubs, 1994.

M33 during 1993 exhibited two denning periods between January and April 1993 that totaled 70 days.

Expanding summer ranges of black bears coincided with increasing temperatures, plant regrowth, and the breeding season. Encounters between adult males and adult females, based on coincident radio locations, were recorded mostly from April through September. Other evidence of a mating season included vaginal swelling, and fresh puncture wounds and lacerations that may have resulted from breeding and fighting for breeding rights (Table 5.5). Coincident radio locations and other evidence of sexual interactions peaked between May and August. In addition, the only family group (consisting of adult female F03 and three radio-collared male cubs) that was monitored in this study dissolved during the month of August (Fig. 5.26). F03 left her 17-month-old cubs in their 1992 summer range before moving five km to the east and an area of abundant oaks and saw palmetto plants. She subsequently denned the following winter in a hollow cypress stump and gave birth to at least two cubs. For most adult bears, summer ranges were usually expansions of winter ranges with considerable overlap between the two areas (Figs. 5.16-5.24).

Florida panthers do not have a distinct breeding season, but mating activities influenced panther movements. Although panthers are physiologically capable of reproducing throughout the year, most births follow an increased period of sexual activity during the winter and early spring (Maehr et al. 1991). This tendency toward higher winter activity may explain the pattern of kitten independence whereby 89% of nine documented family break-ups occurred between November and May (Table 5.6). In several instances, an adult male was in the company of a female panther with kittens

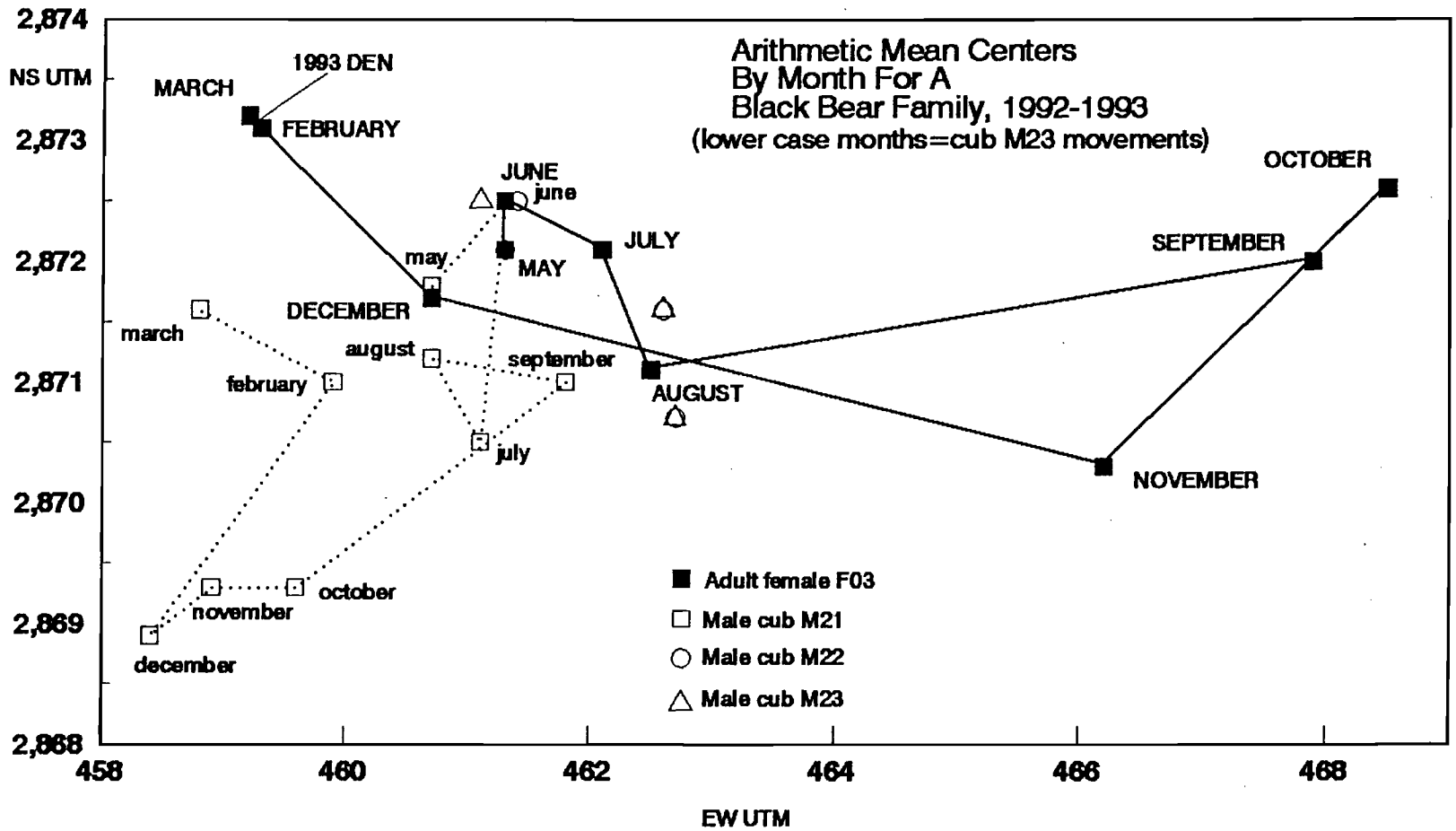


Figure 5.26. Family dissolution of female black bear F03 and three male cubs, 1992.

Table 5.5. Frequency of interactions between male and female black bears in south Florida, 1991-1993, based on coincident radio locations and other factors.

	Month											
	J	F	M	A	M	J	J	A	S	O	N	D
Age group	Number of coincident radio locations between males and females											
All ages	3			1	6	2	5	2	1		1	1
Adults				1	1	2	5	2	1			
Type	Other evidence of a breeding season											
Vulval swelling						1	1	1				
Male wounds						2	4	1		1		1
Female wounds								1				
Total	3			2	7	7	15	6	2	1	1	1

Table 5.6. Characteristics of Florida panther family dissolutions in south Florida, 1986-1993. Independence was defined as the first month during which the arithmetic home range centers of the mother and kitten were >1 km apart. Ages of kittens are in months.

Family groups		Characteristics of litters and separation				
Adult female ID	Kitten ID	Litter size	Date of capture	Kitten age at capture	Month of separation	Age at separation
09	10	1	1/15/86	5	November	16
11	29	1	1/3/89	6	December	18
19	30	4	1/6/89	9	March	12
31	34	3	1/8/90	10	April	13
19	43	1	5/1/90	9	July	13
11	47	1	2/21/92	6	December	17
36	50	2[1]	2/4/92	8	May	11
31	48 & 52	2	5/5/92	6	December	14
40	54	2[2]	2/10/93	10	February	10[3]

[1]Sibling removed for captive breeding program at initial capture
[2]Sibling removed for captive breeding program at an earlier capture
[3]Independence apparently caused by abandonment after #54's first capture

immediately before the family bond dissolved. The average age of kitten independence was 13.8 months (n=9, sd=2.72) and ranged from 10 to 18 months. At least one instance of family break-up was probably caused by the capture of male kitten #54 at 10 months of age. Although female #40 and her kitten (#54) were not found together after the kitten's capture in February 1993 (Fig. 5.27), he survived this early independence and was a resident adult at the time of this writing. In most cases, subadults dispersed from their mothers' ranges immediately after obtaining independence (Figs. 5.28-5.34). However, male #30 remained in his mother's home range for at least six months before dispersing (Fig. 5.35), and kitten #54 localized his activity in the area where female #40 abandoned him.

For black bears of both sexes, increased movements during fall resulted in home ranges that often encompassed the areas used during the previous two seasons, or resulted in convex polygons that were larger and disjunct from them. Telemetry locations during these months were often near or in vegetation communities containing common fruit-producing plants such as saw palmetto, cabbage palm, and live oak. This pattern of fall vagrancy has been observed in many black bear populations (Garshelis and Pelton 1981, Villarubia 1982, Rogers 1987a), and is related to the availability of high-energy food sources that often are clumped and disjunct from winter and summer ranges (Eagle and Pelton 1983). Some bears, however, did not always exhibit consistent patterns of inflated fall home ranges such as M08, and M13 during 1992 and 1993. This may be attributable to annual variation in food abundance despite my observation that staple foods such as fruits of saw palmetto and cabbage palm may vary among individual plants but locally appear to produce annually stable supplies. Further, neither bear inhabited an area where

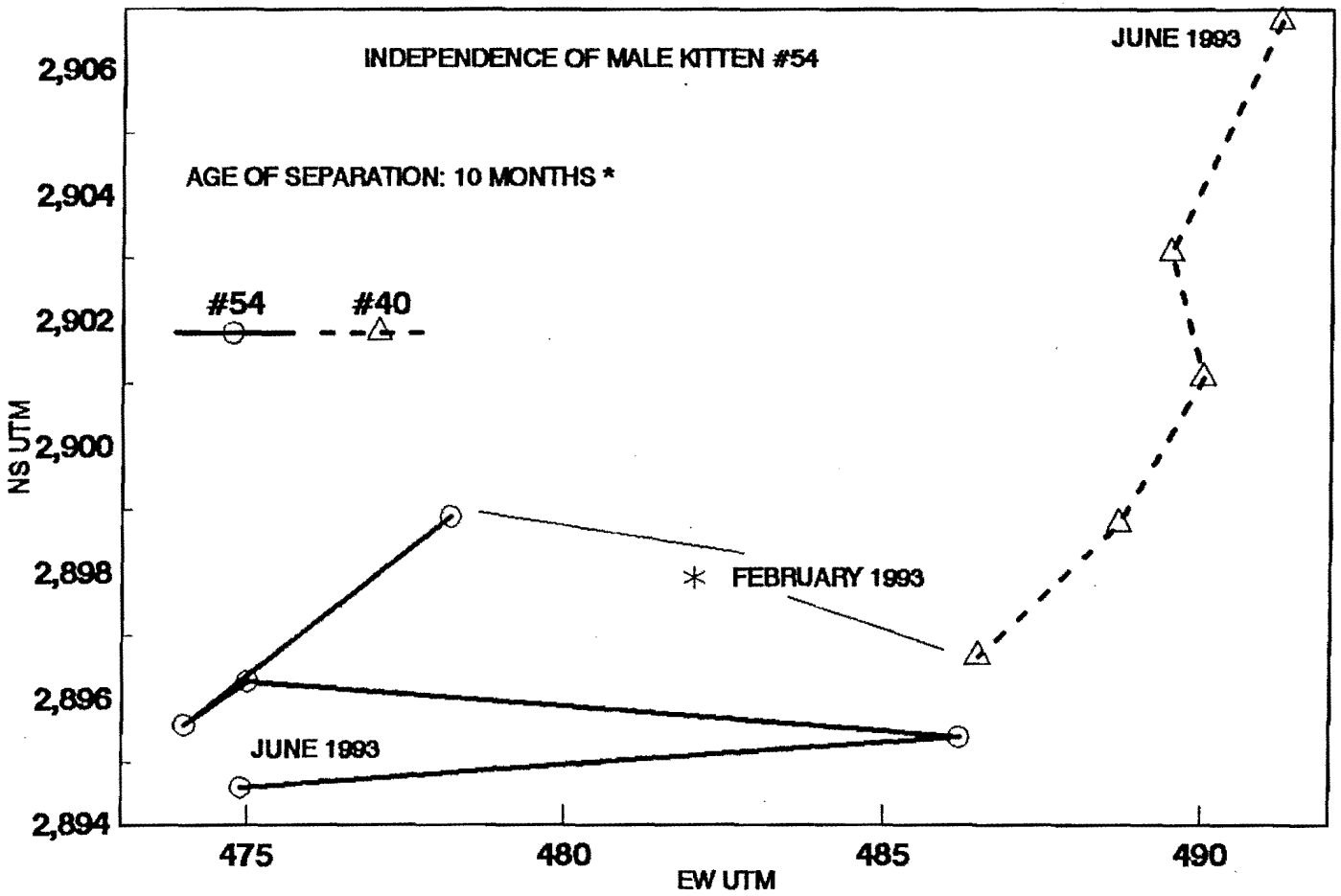


Figure 5.27. Family dissolution of female panther #40 and 10-month old male kitten #54, 1993.

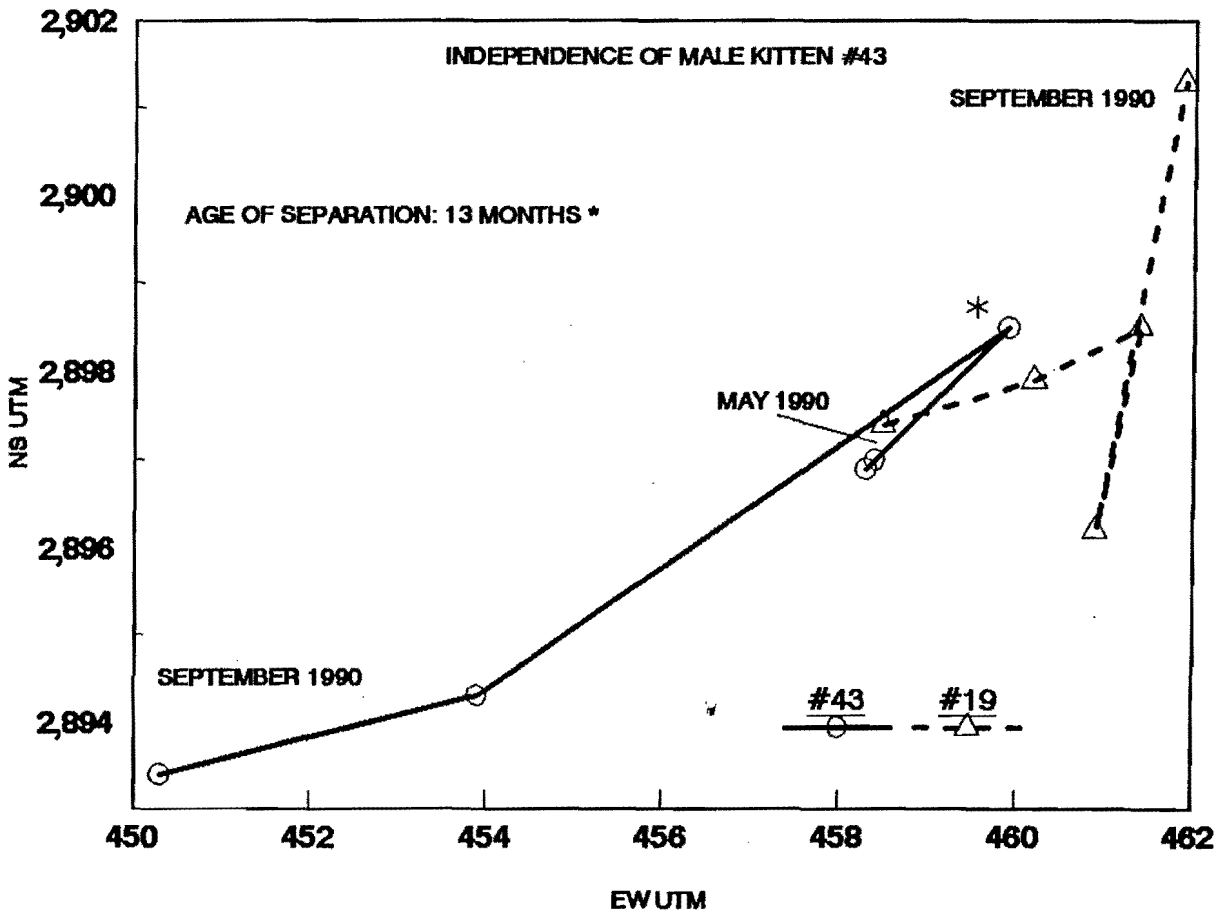


Figure 5.28. Family dissolution of female panther #19 and 13-month old male kitten #43, 1990.

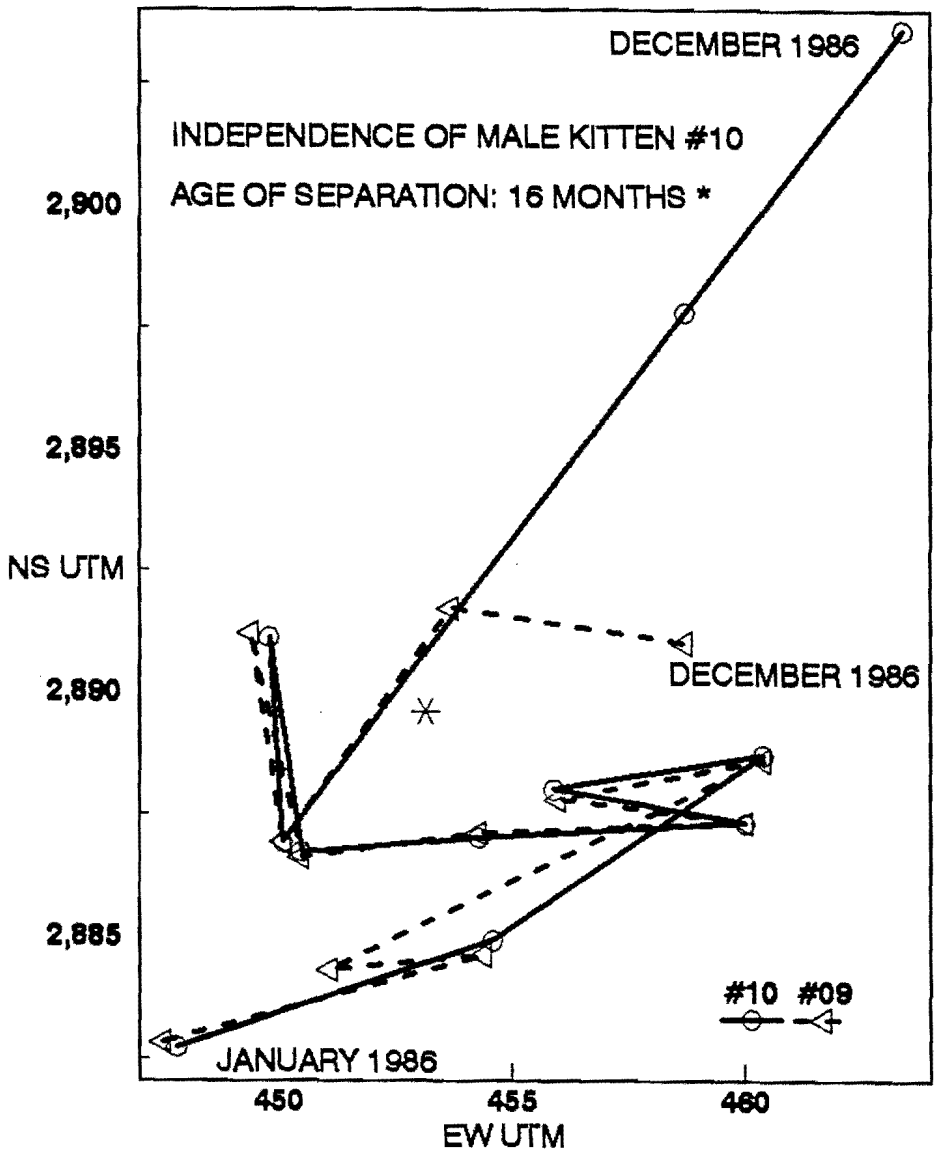


Figure 5.29. Family dissolution of female #09 and 16-month old male kitten #10, 1986.

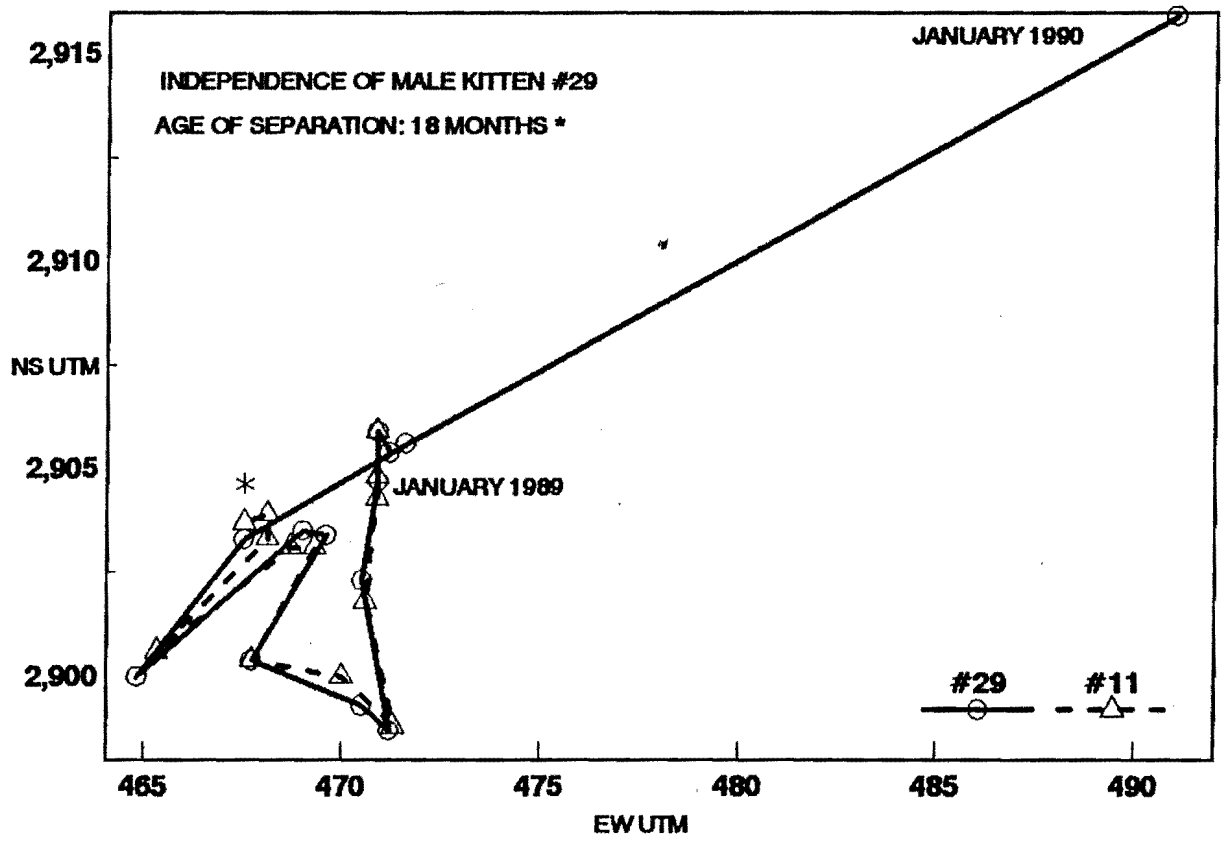


Figure 5.30. Family dissolution of female panther #11 and 18-month old male kitten #29, 1990.

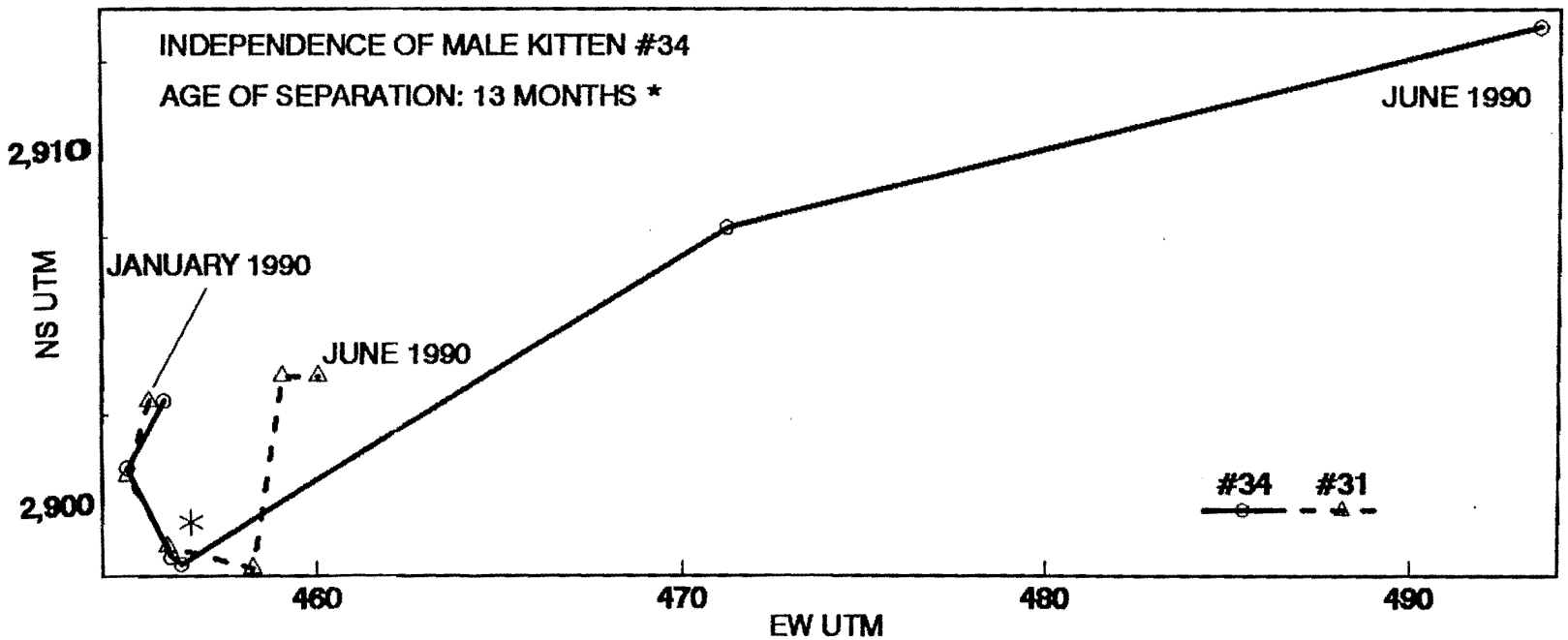


Figure 5.31. Family dissolution of female panther #31 and 13-month old male kitten #34, 1990.

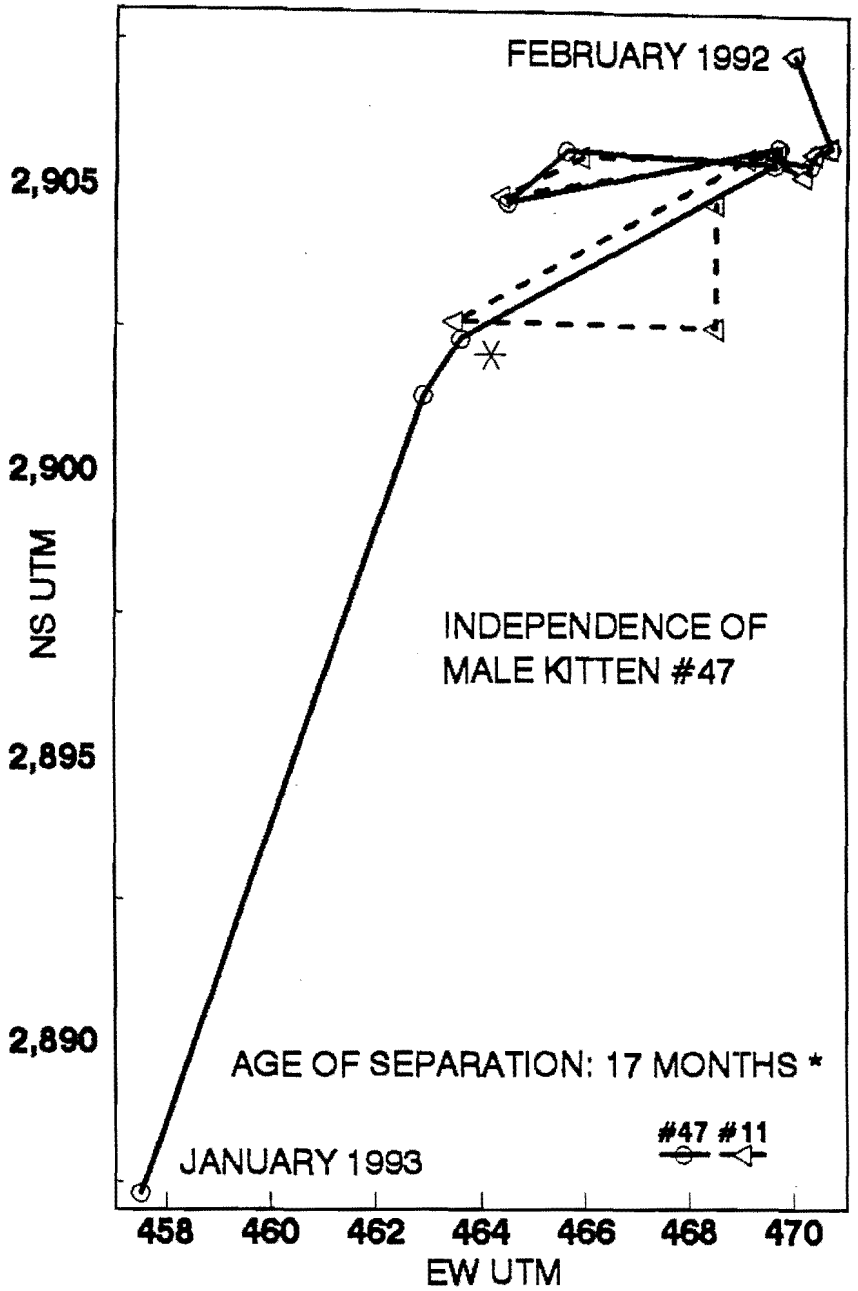


Figure 5.32. Family dissolution of female #11 and 17-month old male kitten #47, 1992.

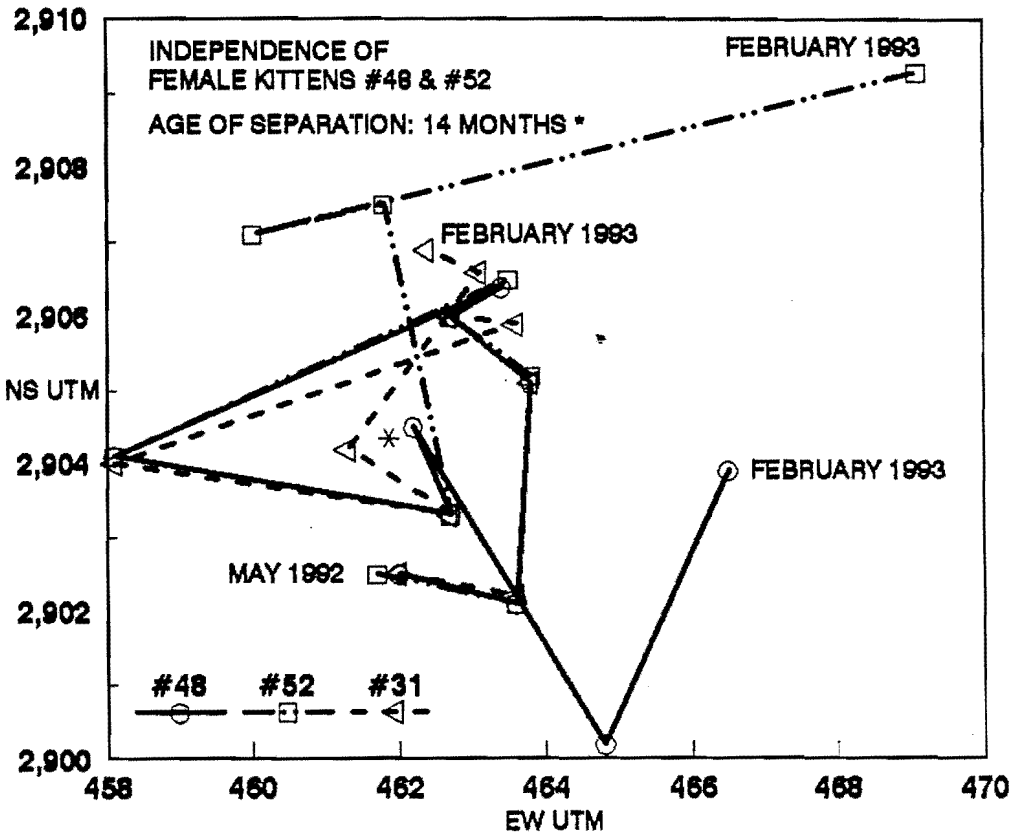


Figure 5.33. Family dissolution of female #31 and 14-month old female kittens #48 and #52, 1993.

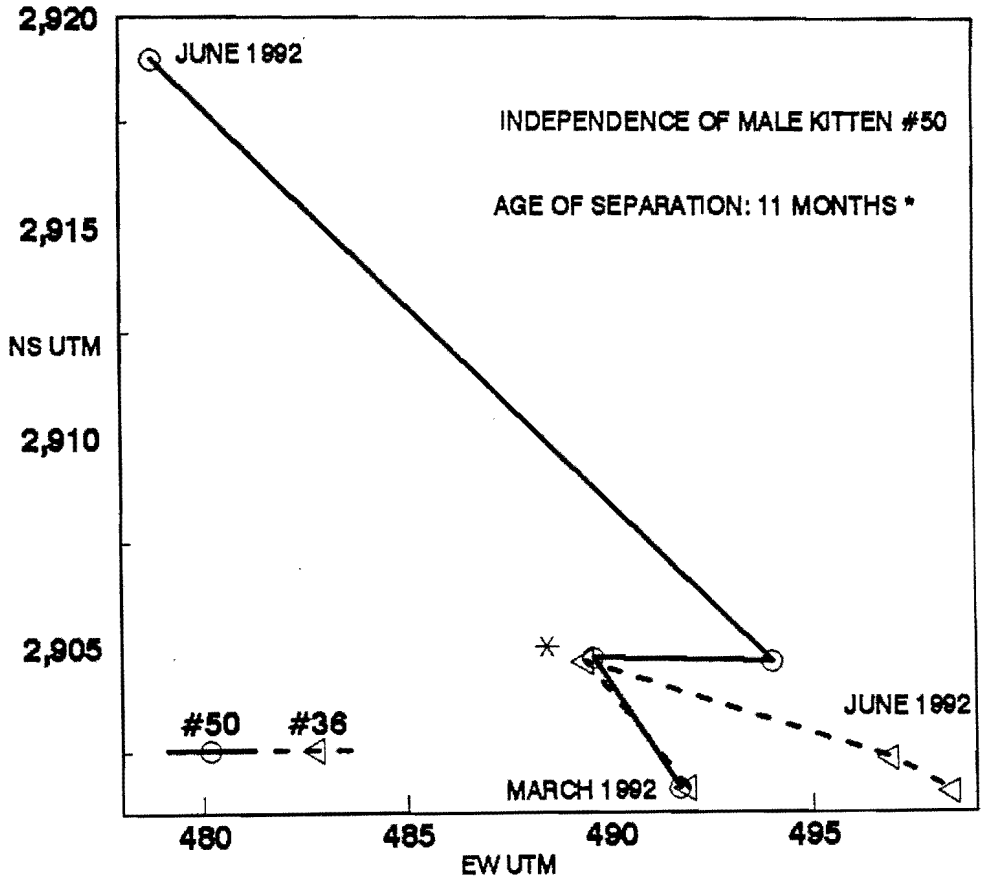


Figure 5.34. Family dissolution of female #36 and 11-month old male kitten #50, 1992.

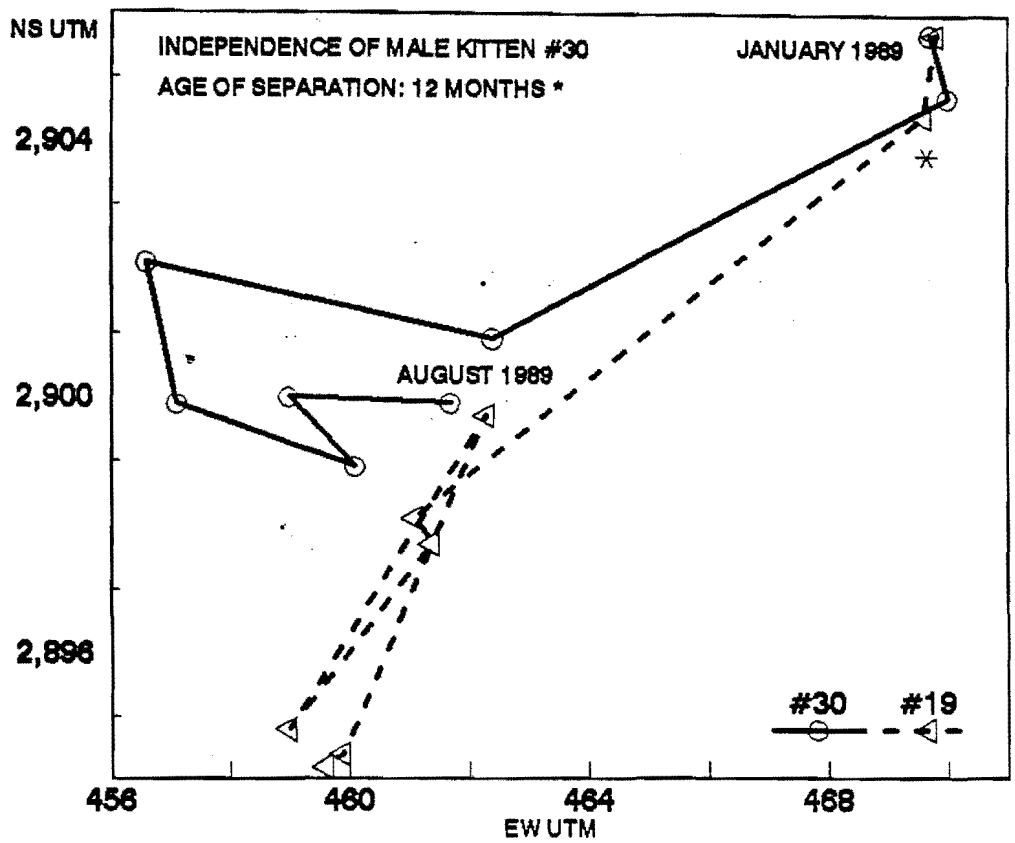


Figure 5.35. Family dissolution of female #19 and 12-month old male kitten #30, 1989.

commercial saw palmetto fruit-collectors decimated food supplies in order to provide the raw material for pharmaceutical products (Murray 1994). In south Florida, adult black bear home ranges were not only larger during fall, but they could be separated by more than 20 km from summer ranges (Figs. 5.36-5.39). In several cases, particularly adult male M06 (Fig. 5.37), the shift from a summer to fall range occurred quickly (i.e. <3 days). In this case, the bear left a summer range dominated by mixed swamp vegetation in favor of pine flatwoods containing extensive thickets of saw palmetto. Bear scats collected in this area confirmed that fruit of saw palmetto was consumed nearly to the exclusion of other foods. The rapid movements of M06 to his disjunct fall range suggest that he was previously familiar with this clumped food supply. Such learning may be important to maximizing mass growth and in building fat supplies; factors that are of particular importance to pregnant females that den by late January, give birth in late winter, and emerge with cubs in mid-April following a two-three month fast.

Home Range Fidelity and Replacement

While seasonal patterns in home range size were examined for all three species, only panthers were monitored adequately to examine the process of resident senescence and home range replacement. Maehr et al. (1991) observed that through 10 years of radio tracking, the permanent abandonment of a home range was rare. Adult female #09 left a home range in the southern Golden Gate Estates and colonized the vacated home range created by the removal of non-reproductive female #08 in 1987 (Fig.5.40). Her subsequent litter consisted of two kittens; twice the number of kittens produced by her in each of two previous litters. Since the removal for captive breeding of these two male kittens in 1991, #09 continues to occupy the same home range but has not reproduced

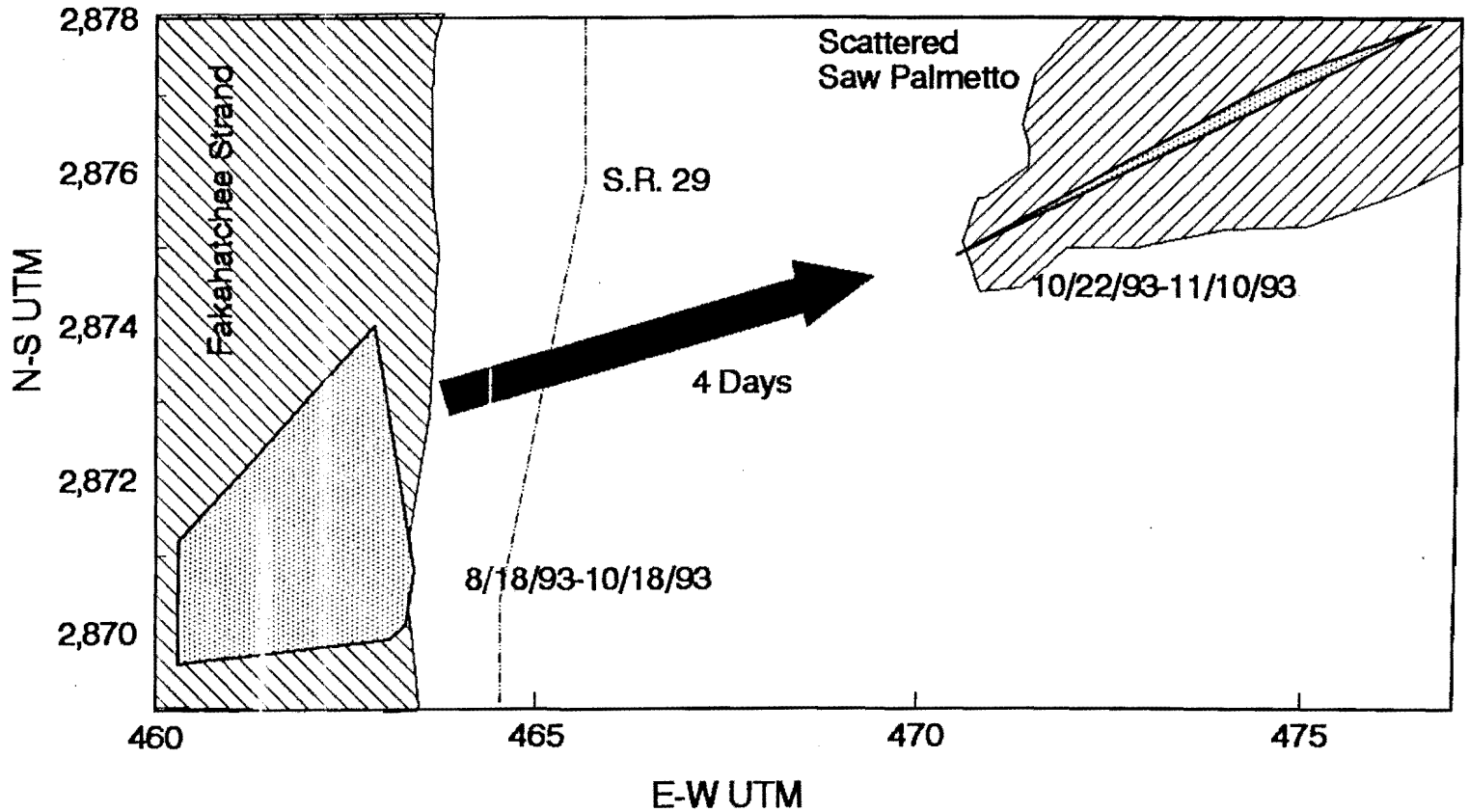


Figure 5.36. Home range shift from summer to fall of female black bear F03 during 1993.

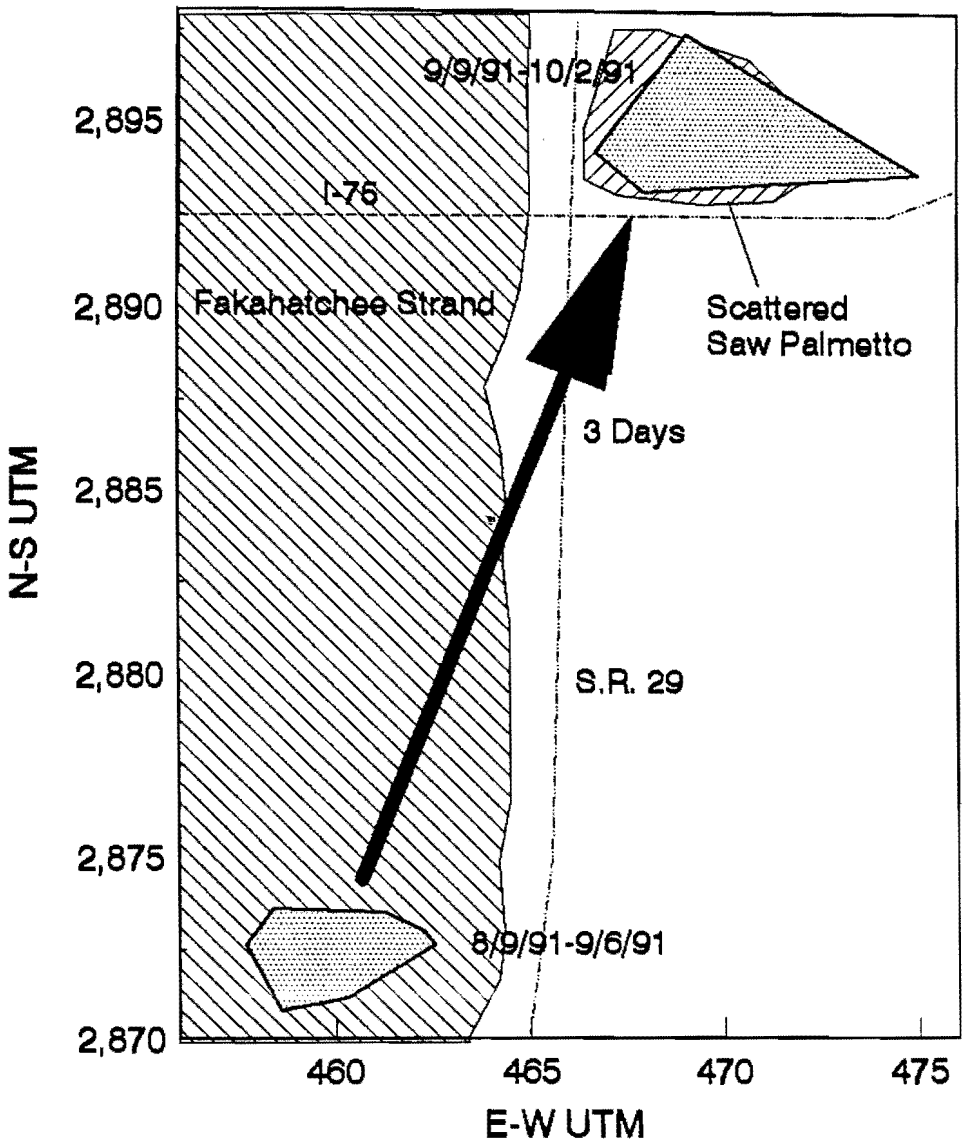


Figure 5.37. Home range shift from summer to fall of male black bear M06 during 1991.

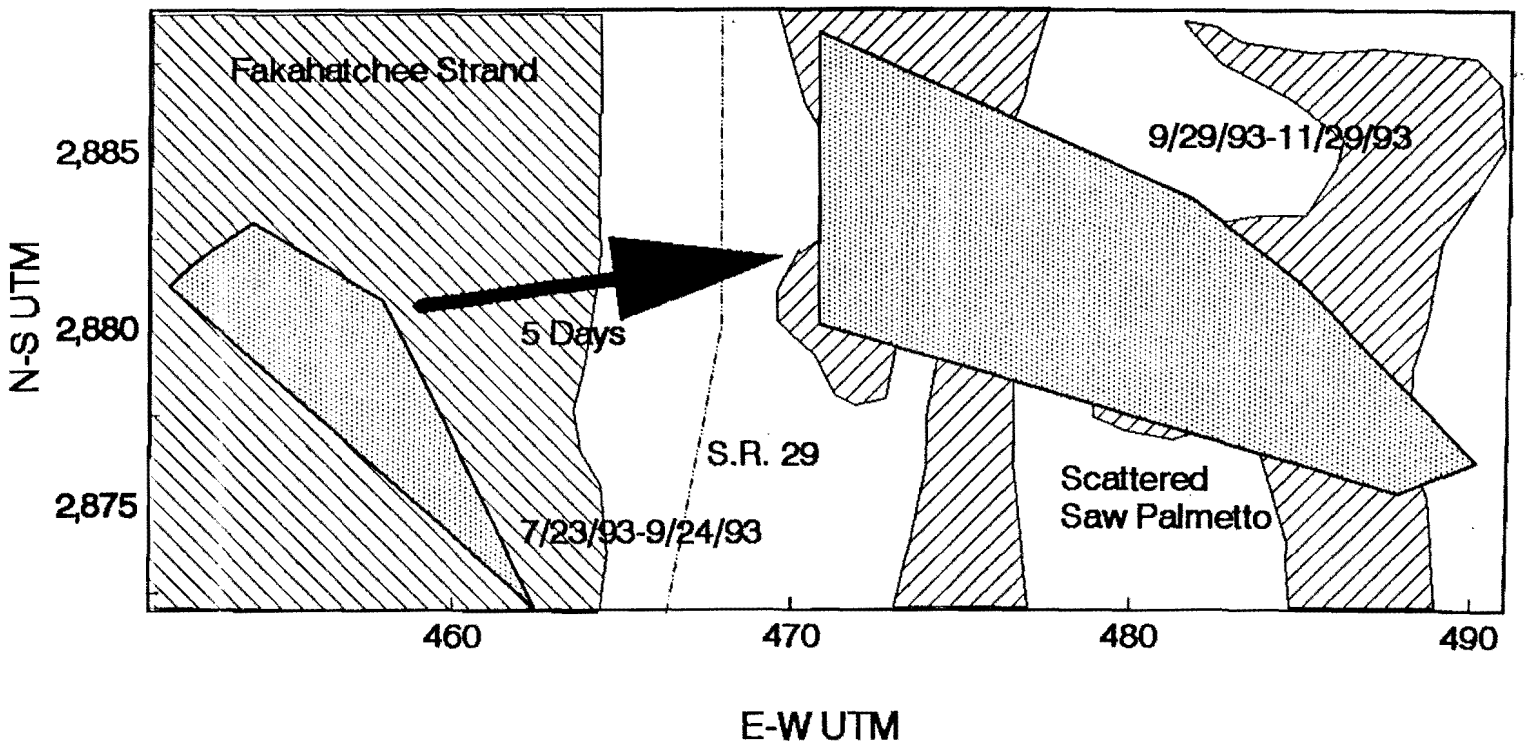


Figure 5.38. Home range shift from summer to fall of male black bear M35 during 1993.

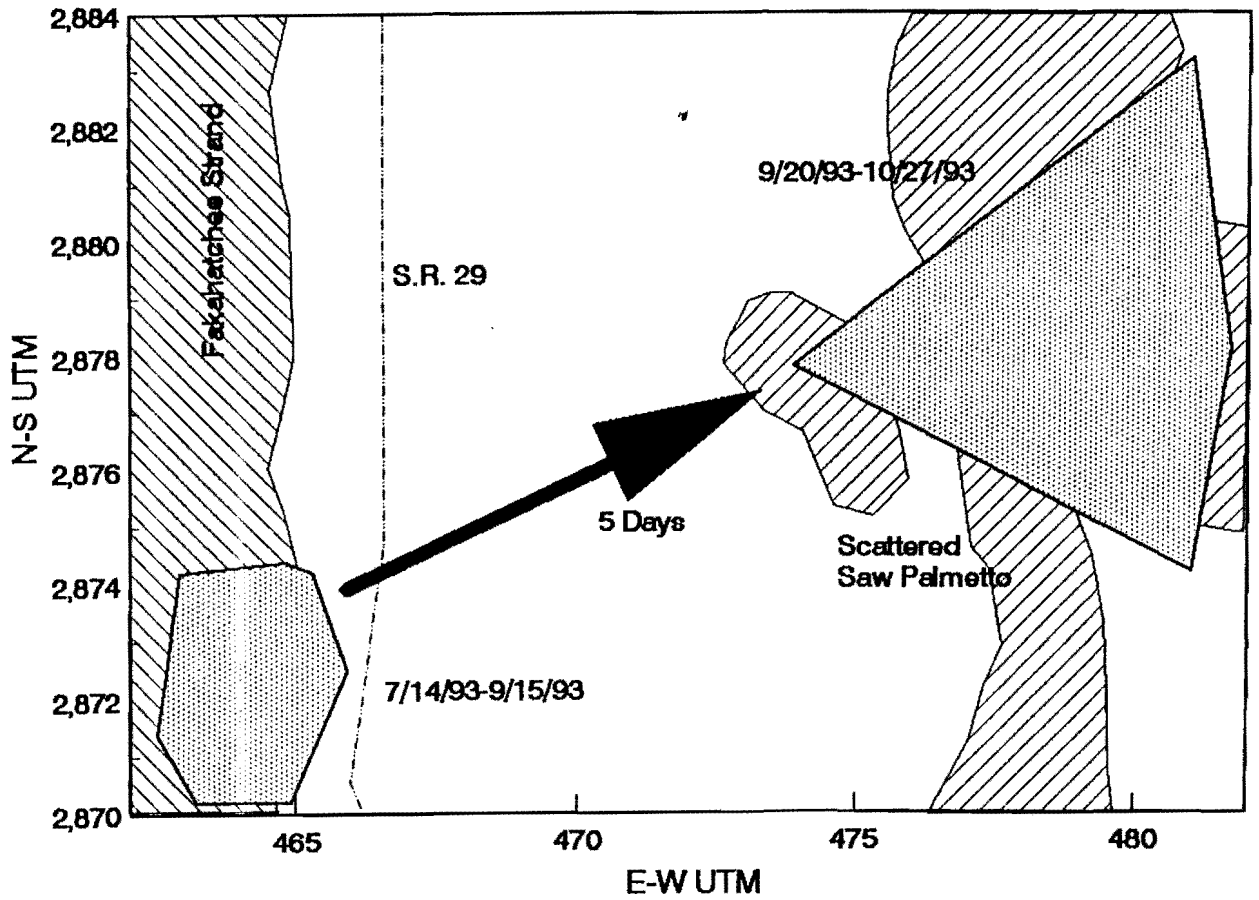


Figure 5.39. Home range shift from summer to fall of male black bear M36 during 1993.

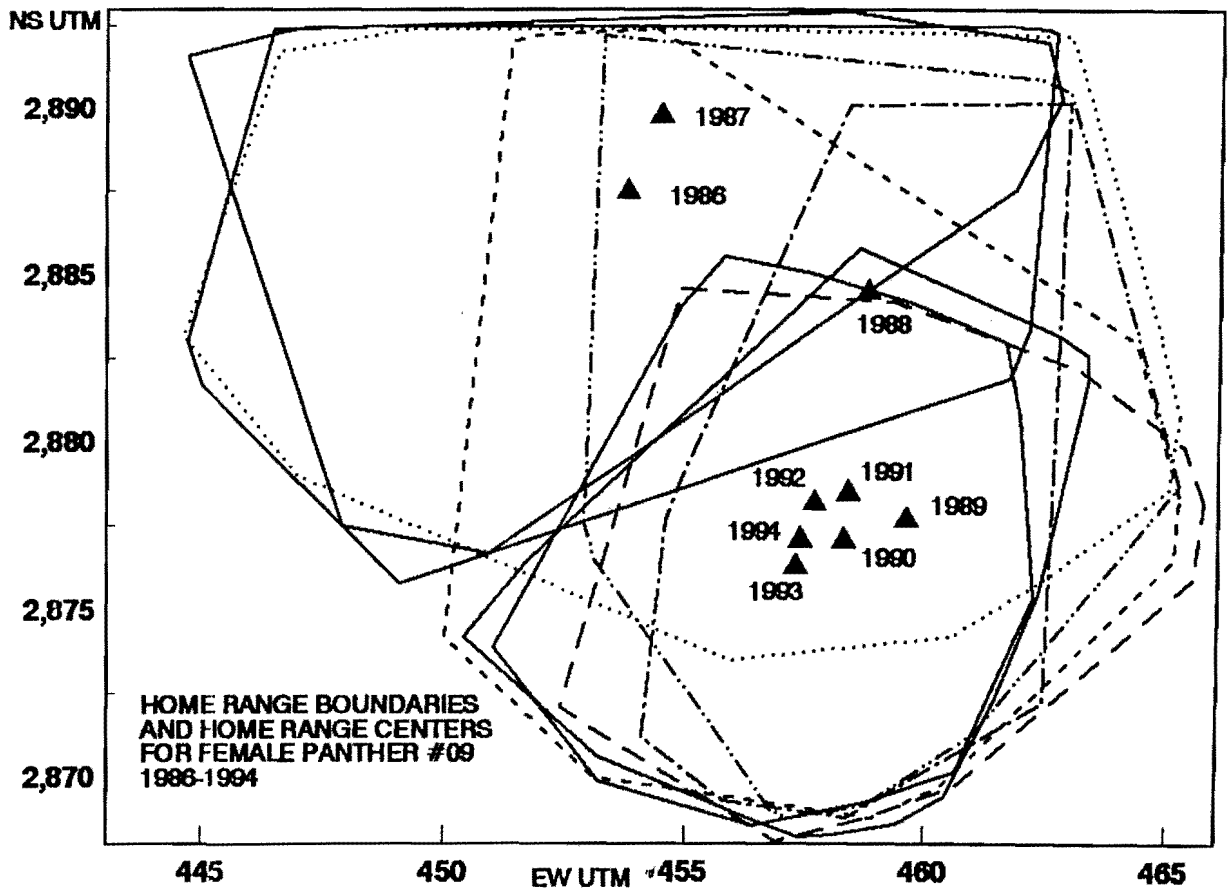


Figure 5.40. Annual home range boundaries and arithmetic home range centers for female panther #09 from 1986 through 1994.

(possibly as the result of reproductive senescence at 10-11 years of age). Thus, like the tenure of female #08 in the same location, successful reproduction is not a key element for maintaining a resident home range even though the quality of that home range may enhance the reproductive fitness of a younger female. Adult female #19 raised her first litter in her mother's home range before dispersing and establishing a new breeding territory adjacent to her natal range (Fig. 5.41, Maehr et al. 1989b). Male panther #26, although considered an adult when captured in 1988, was not documented as a breeder until he filled a home range vacancy created by the death of male #17 in 1990 (Fig. 5.42). The turnover of this home range to a new resident occurred amid a complex arrangement of subadult males and non-resident adults that lived at the periphery of occupied panther range in eastern Collier County (Fig. 5.43). It is possible that failing health of male #17 was recognized by as many as four other males, which may explain the temporarily high density of males in this area from 1991 through 1992. The pattern for most adults, however, was to maintain home ranges with stable home range centers over many years (Figs 5.44-5.51).

Resident male home ranges appear to occupy the same space regardless of the occupant. The shapes of such traditional home ranges are likely a function of the distribution of dense forested cover and the distribution of females. However, adult male #16 continued using Everglades National Park for five years after the deaths of all documented females in that subpopulation (O.L.Bass pers. comm.), suggesting that familiarity with a home range may encourage fidelity to it. Telemetry data collected from the Fakahatchee Strand exemplify the concept of the traditional home range in as much as at least five adult males have occupied this distinct vegetative system from 1981 through

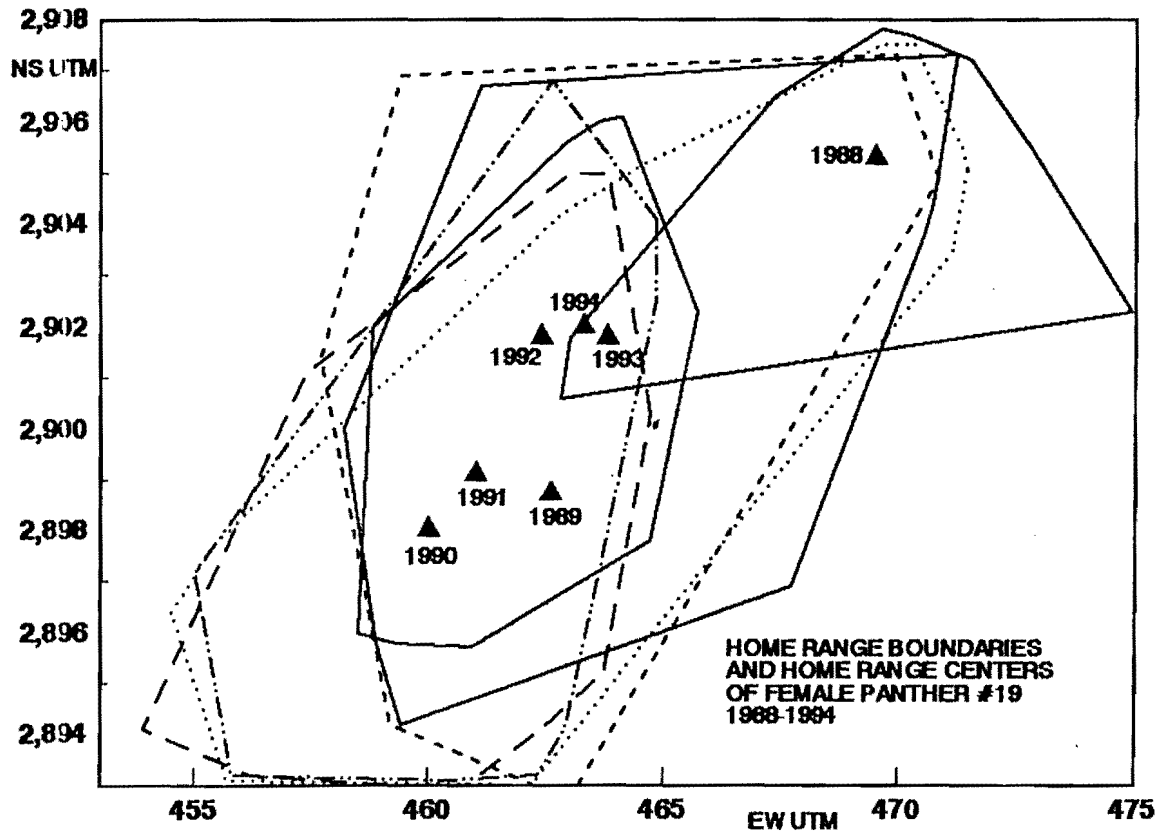


Figure 5.41. Annual home range boundaries and arithmetic home range centers for female panther #19 from 1988 through 1994.

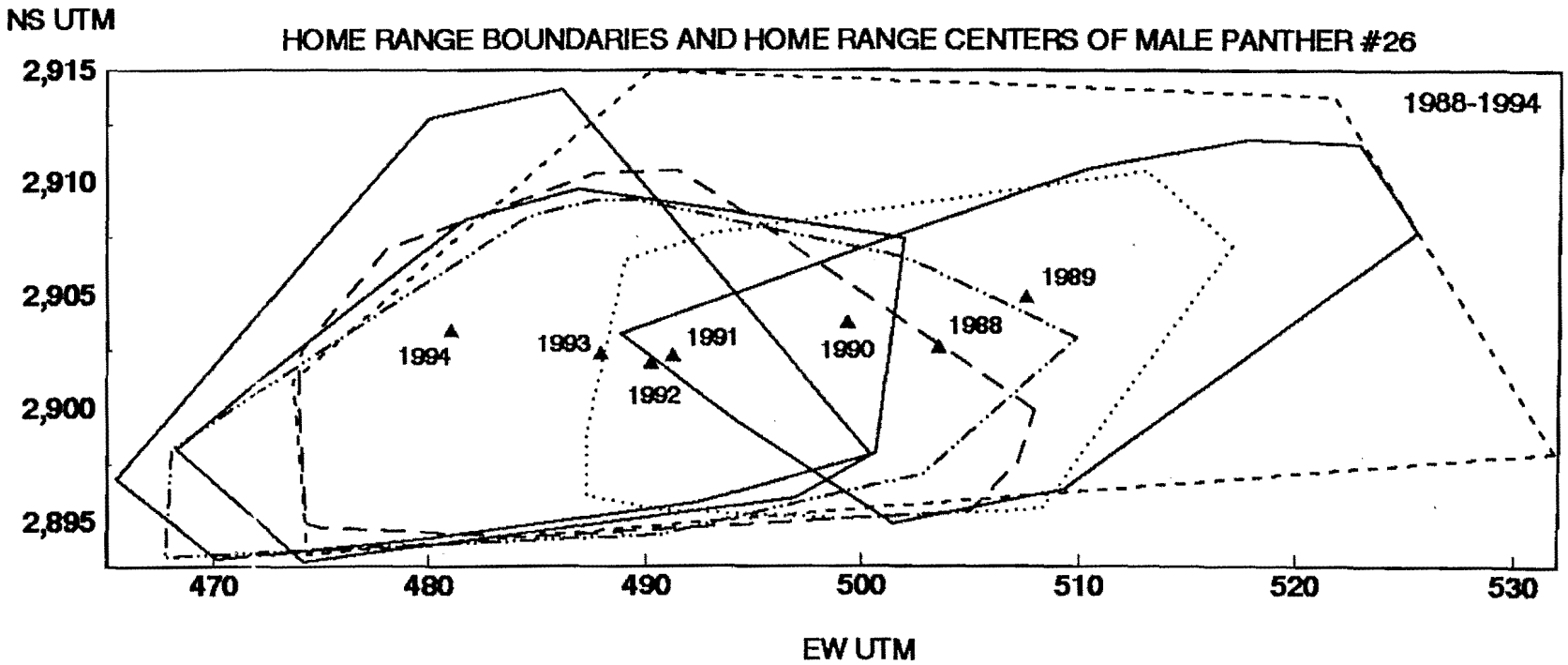


Figure 5.42. Annual home range boundaries and arithmetic home range centers for male panther #26 from 1988 through 1994.

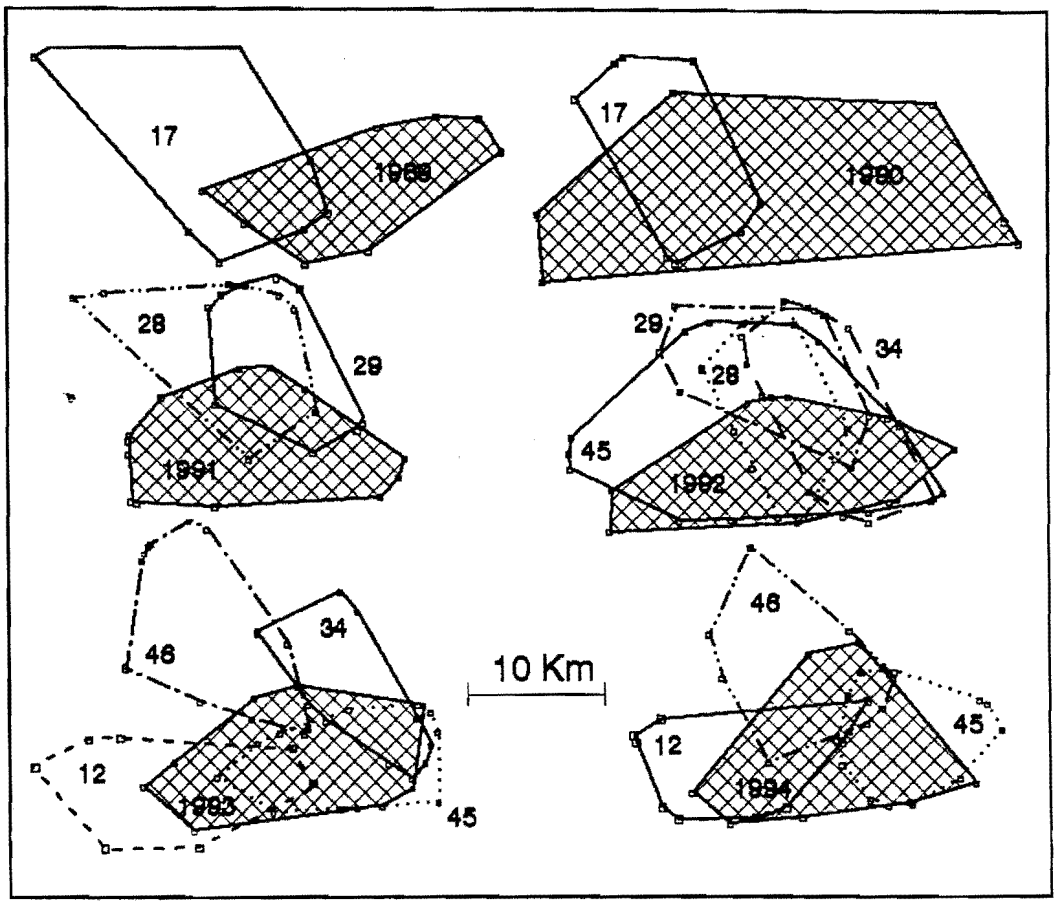


Figure 5.43. Home range expansions and home range shifts of male panther #26 relative to potential male competitors from 1989 through 1994.

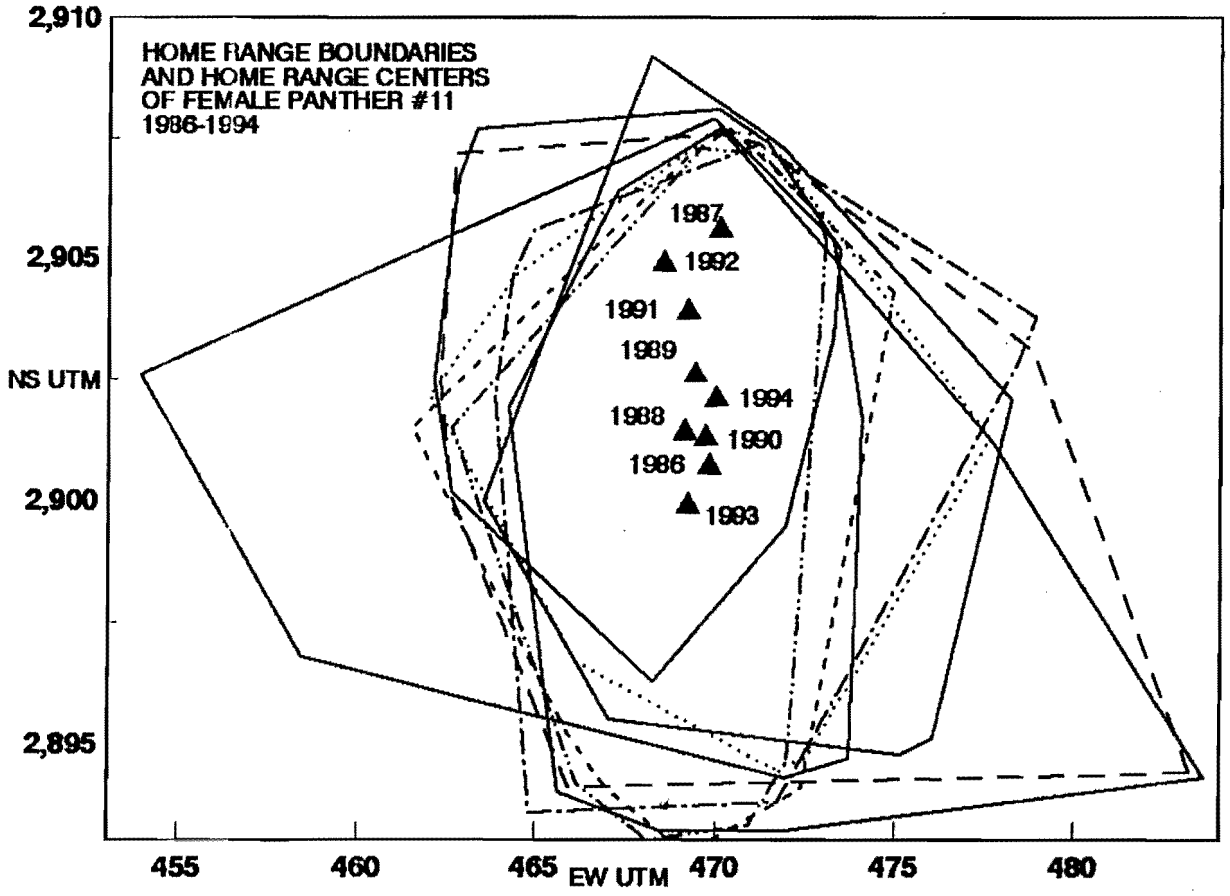


Figure 5.44. Annual home range boundaries and arithmetic home range centers for female panther #11 from 1986 through 1994.

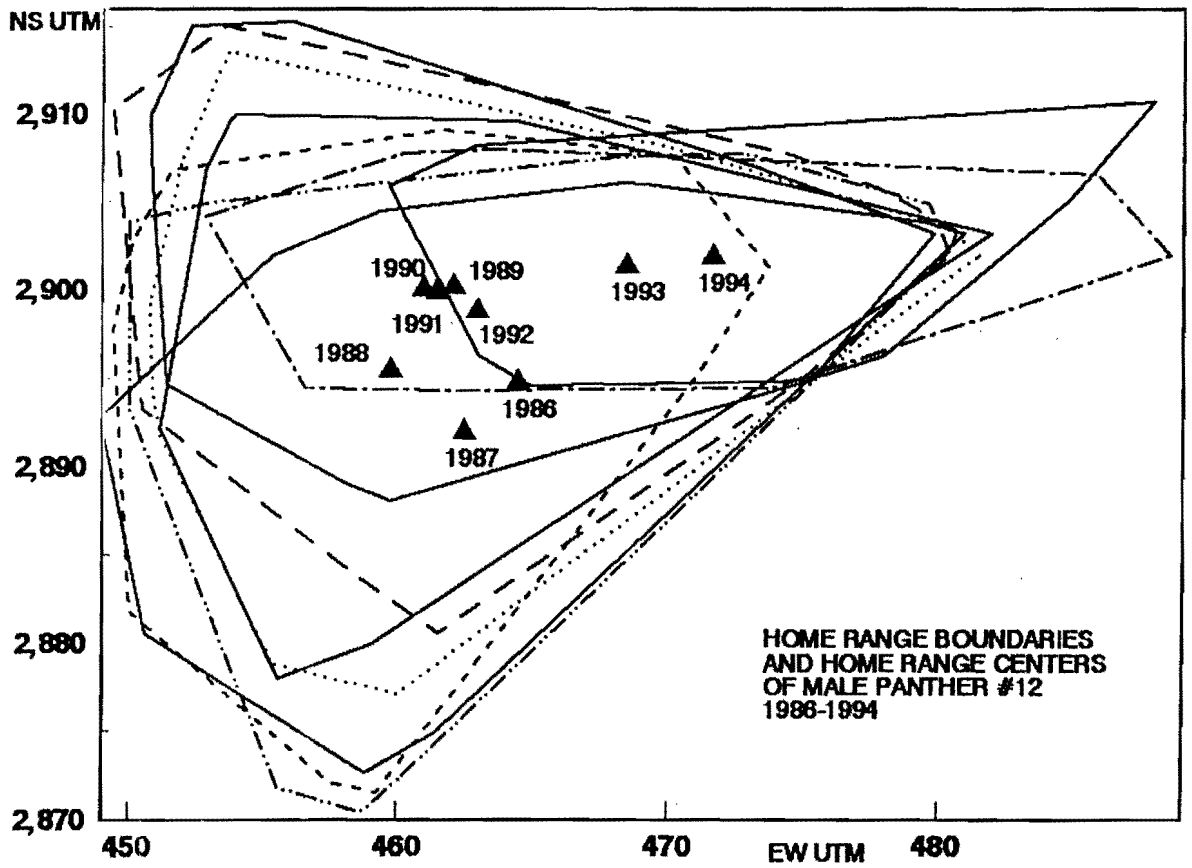


Figure 5.45. Annual home range boundaries and arithmetic home range centers for male panther #12 from 1986 through 1994.

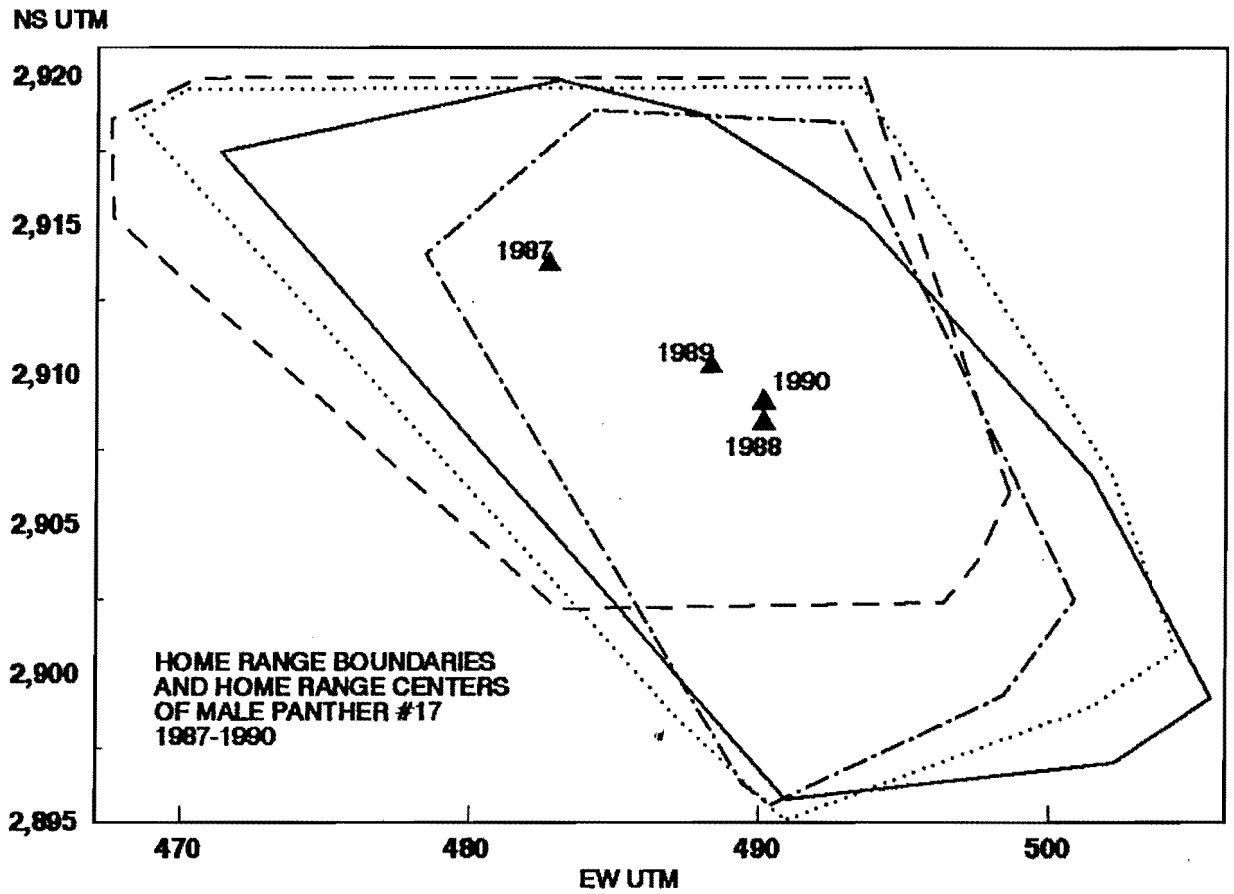


Figure 5.46. Annual home range boundaries and arithmetic home range centers for male panther #17 from 1987 through 1990.

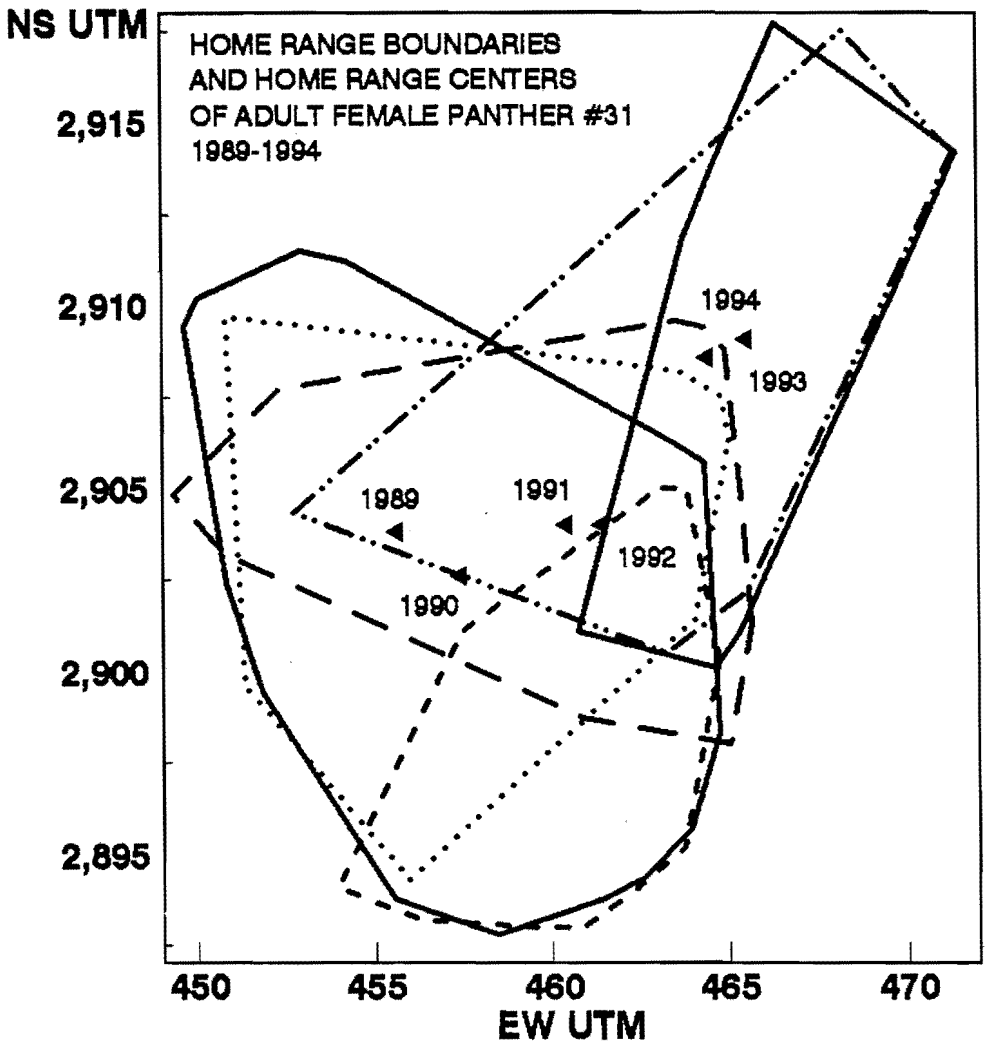


Figure 5.47. Annual home range boundaries and arithmetic home range centers for female panther #31 from 1989 through 1994.

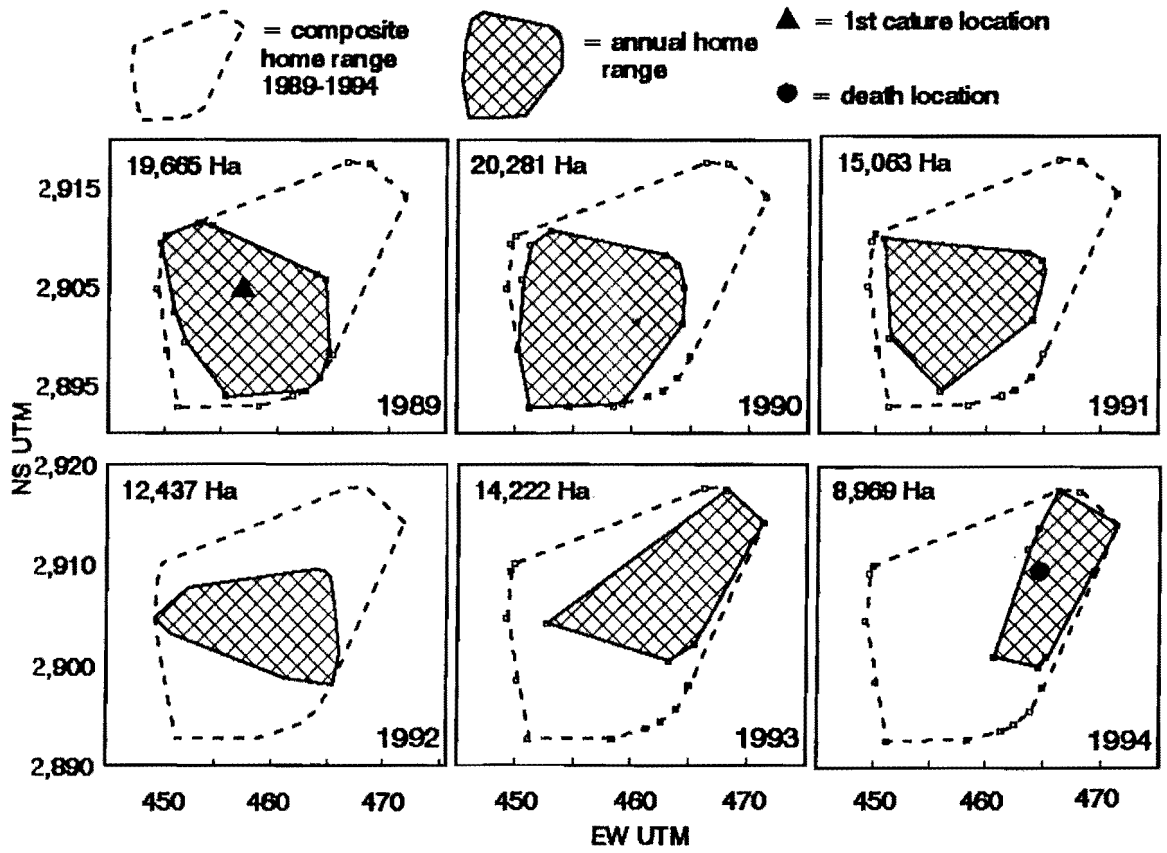


Figure 5.48. Home range dynamics relative to a six-year composite home range of adult female panther #31, 1989-1994.

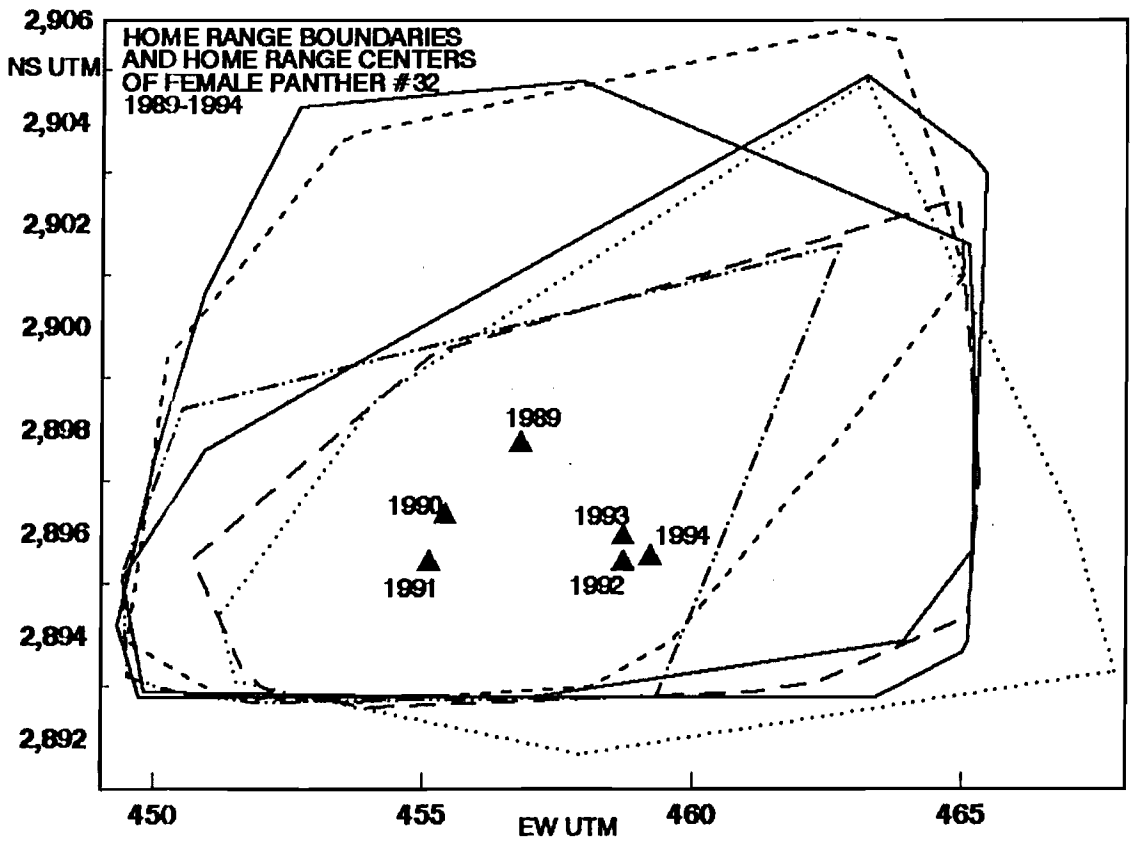


Figure 5.49. Annual home range boundaries arithmetic home range centers of female panther #32, 1989-1994.

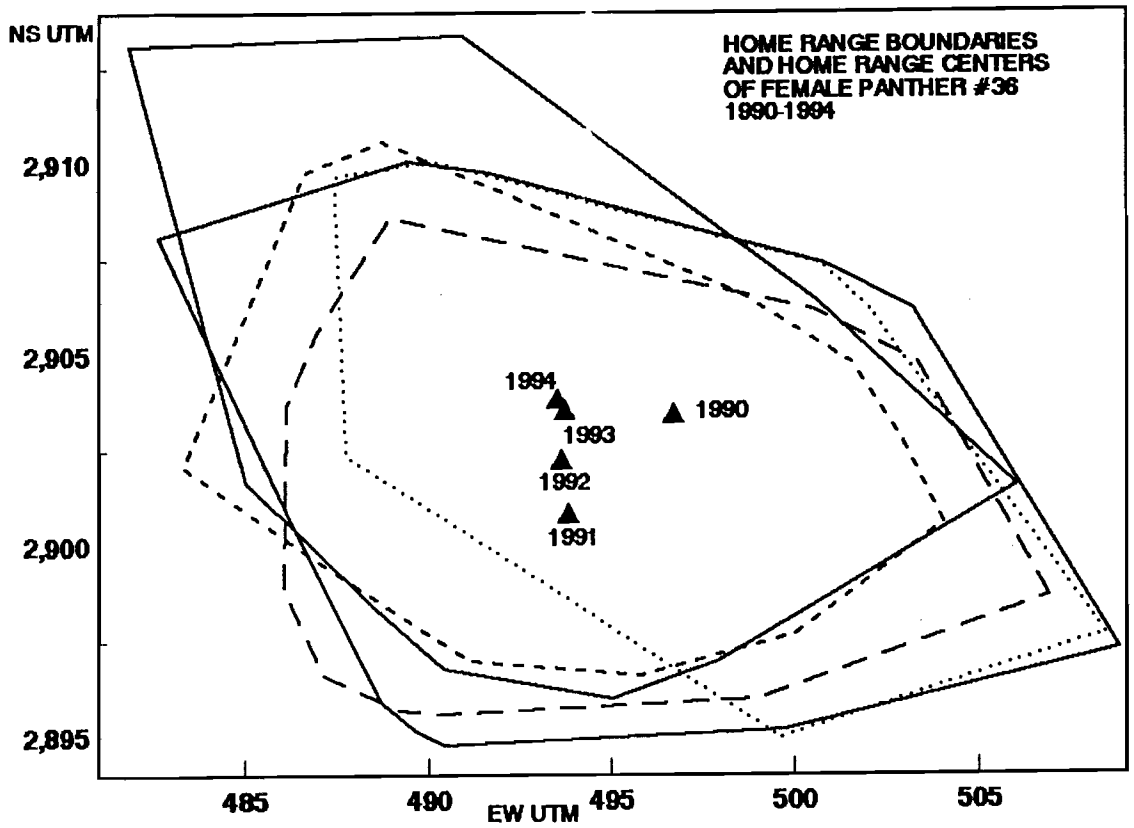


Figure 5.50. Annual home range boundaries arithmetic home range centers of female panther #36, 1990-1994.

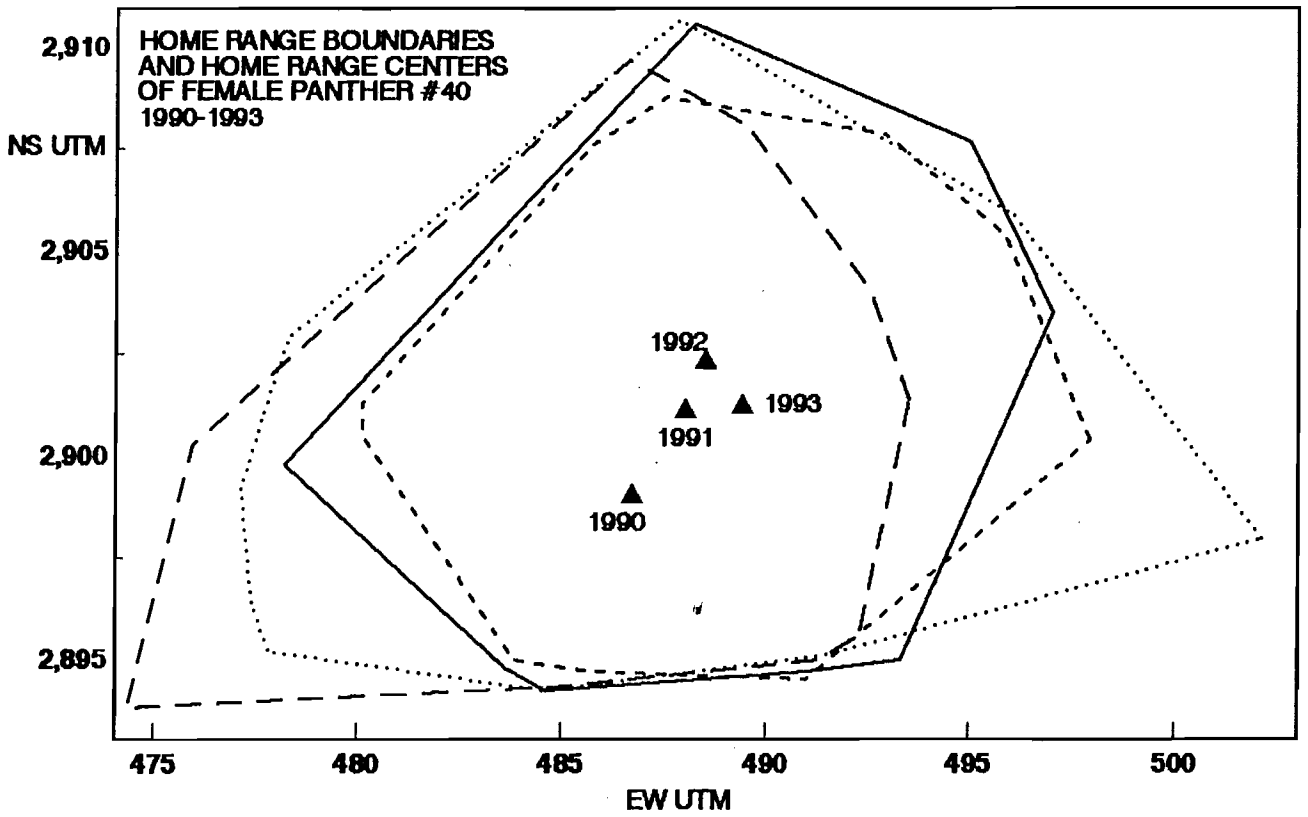


Figure 5.51. Annual home range boundaries arithmetic home range centers of female panther #40, 1990-1993.

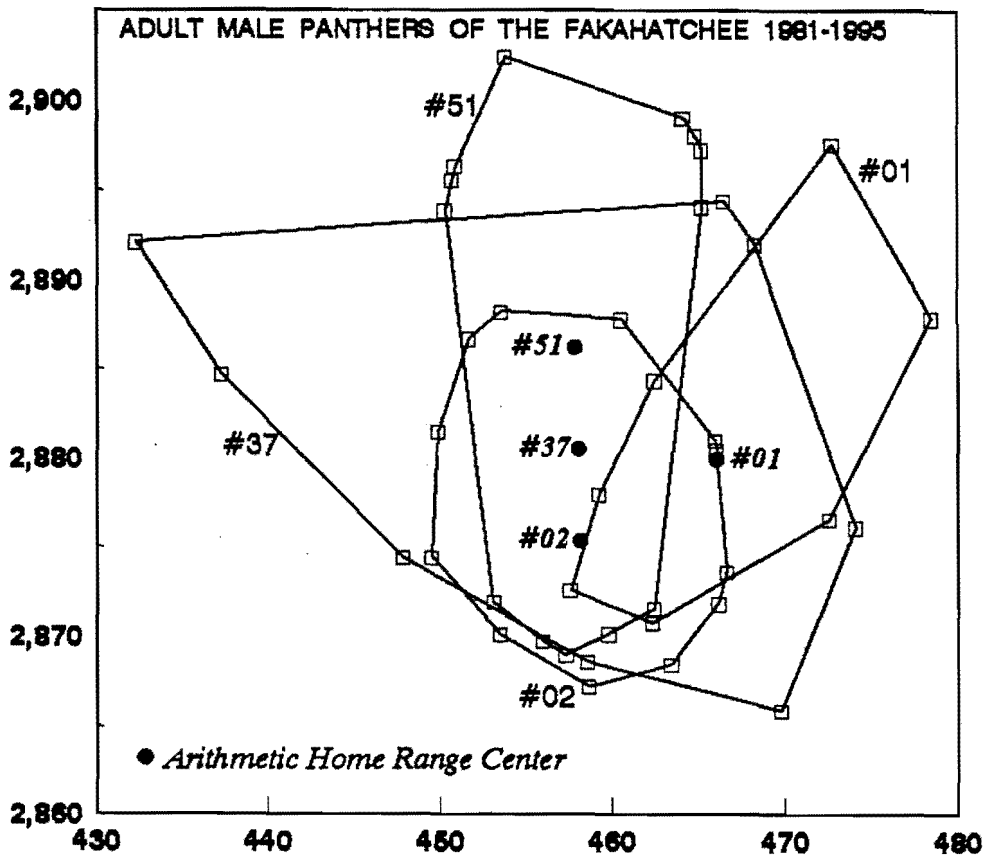


Figure 5.52. Annual home range boundaries and arithmetic home range centers of resident adult males in the Fakahatchee Strand, 1981-1994.

1994, with little variation in the shapes and arithmetic mean centers of these home ranges (Fig. 5.52). Whether the deaths were caused by highway collision or intraspecific aggression, a replacement for the lost resident appeared quickly, and no interruptions to local reproduction were observed.

Resident male #12 demonstrated site fidelity for over eight years, and interacted with at least 6 adult females during this time span. His home range boundaries expanded and contracted occasionally, but his center of activity remained relatively stable (Fig. 5.53). Contractions coincided with the presence of other adult males such as male #37, and male #51. After #37's death from highway collision, #12's home range expanded to recolonize the area previously ceded to #37. The appearance of male #51 in 1992 preceded another home range withdrawal by #12 from the southern Fakahatchee Strand. He was subsequently killed by adult male #46 in an area that #12 had not used during eight previous years of study. In this case, I suspect that failing health reduced the ability of #12 to adequately patrol the entirety of his long-standing home range, and became vulnerable to the aggression of competing males which previously had been successfully repelled or killed.

Bears were insufficiently studied to allow the characterization of individual home range dynamics over time. However, the sample of adult male black bears was sufficiently large that a comparable range of ages could be contrasted with male panther #12. An examination of panther #12's annual home range sizes reveals the fluctuations caused by neighboring individuals and the declines associated with failing health (Fig. 5.54). A comparable pattern of relatively constant home range size in male black bears is also apparent from four to 11 years of age. This was then followed by older animals with

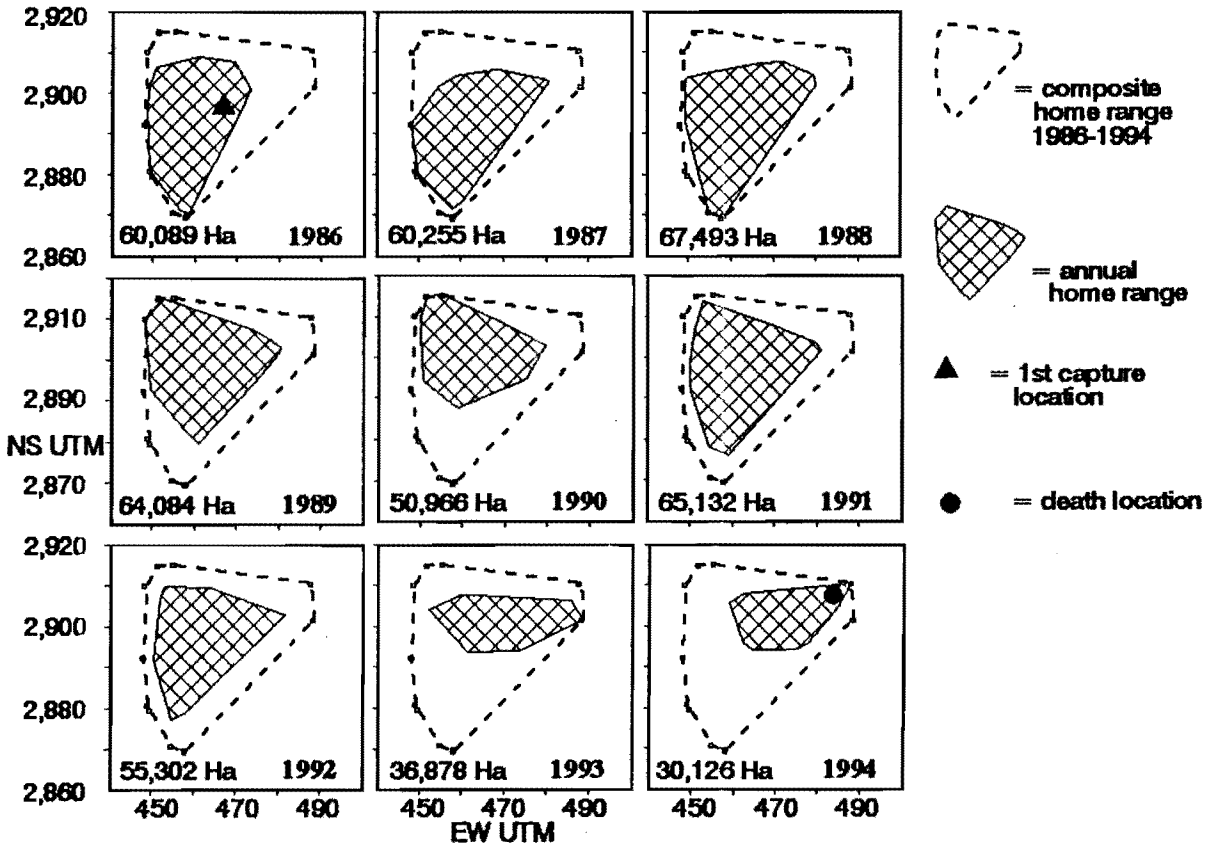


Figure 5.53. Annual home range dynamics of resident male panther #12, 1986-1994.

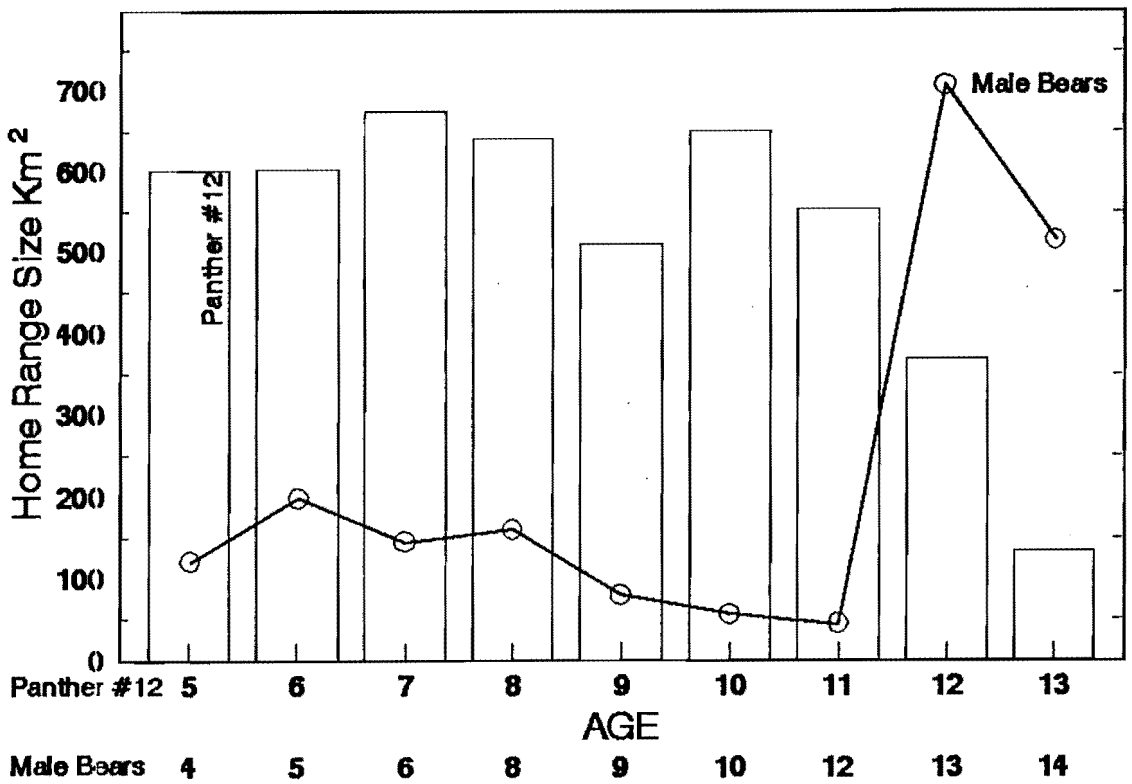


Figure 5.54. Annual home range sizes of male panther #12 from five to 13 years of age compared to home range sizes of black bears of similar ages.

larger home ranges; a distinct contrast to the pattern exhibited by panther #12. While this comparison is confounded by the variation inherent among individual bears and the quality of habitat within which their home ranges are distributed, it does suggest that adult male age results in different spatial patterns between the two species. Because panthers exhibit a life style that is continually violent (i.e. prey procurement, territory defense) and individual fitness is dependent upon the ability to kill large prey and defend territories from competitors, minor injuries and senility likely have significant influences on the ability to maintain dominance of a home range. Black bears, on the other hand, do not require agility or strength to maintain adequate nutrition, and there was no evidence that male black bears continually defend territories against other males (fighting seemed to be restricted to the breeding season and may have been related to individual females, not territories). Further, advancing age in black bears may afford some advantage in that older individuals may have greater experience with patterns of food distribution, and thus, may be more efficient in their use of the landscape. The larger home range sizes of older bears, may simply be related to a better knowledge of alternate food sources.

Overlap Within and Among Species

Patterns of home range overlap among Florida panthers were similar to the arrangement of resident adults described by Maehr et al. (1991)(Fig. 5.55). Indeed, nine out of 13 residents monitored in 1991 were still occupants of the same areas in 1993. With the exception of the southern Fakahatchee Strand and female #09, overlap among females was high, whereas males overlapped only at the peripheries of their home ranges. The greatest difference in panther home range distribution between 1991 and 1993 was the colonization by female #52 of a part of the Okaloacoochee Slough on private land

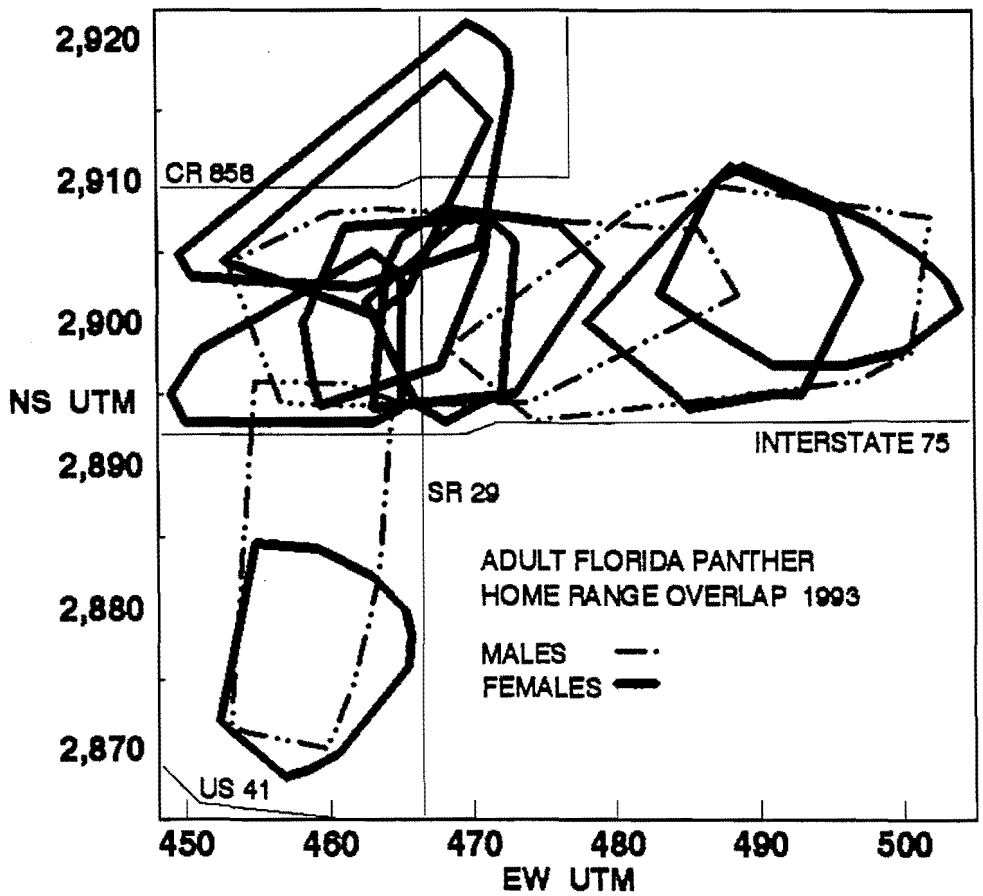


Figure 5.55. Home range overlap of resident adult panthers in southwest Florida during 1993.

where female occupation had not previously been documented. Florida panthers clearly exhibited the characteristics of a land tenure system that has been reported for the species throughout its range.

The duration of the study was insufficient to determine definitive patterns in land tenure among black bears in south Florida. Nor were examples of home range replacement documented. However, resident adult females exhibited home range fidelity from year to year, particularly during winter and summer. Variation within females between years during fall was likely a product of the biannual cycle of cub-rearing. Females with large fall home ranges likely were traveling without cubs. Adult males monitored more than one year exhibited consistent movement patterns between years, punctuated by annual fall peregrinations. After the first full year of radio-tracking 14 adult black bears, home range distribution and overlap suggested a landscape that supported varying densities of adults with gaps between groups of individuals (Fig. 5.56). With 15 additions to the adult sample in 1993 (Fig. 5.57), the distribution of home ranges filled in the apparent gaps observed in 1992. Distribution of collared female home ranges was more a reflection of trap site location than demography. Their smaller home ranges made females less vulnerable to capture because trap sites were not concentrated enough to sample all individuals in the study area. Females were probably as evenly distributed across the landscape as males, but wider movements increased the likelihood that males would span the distances between trap locations. Overlap between and within genders ranged from entire to minimal, with as many as five individuals overlapping each other. In no case was there an impression that all of the bears between trap sites had been captured,

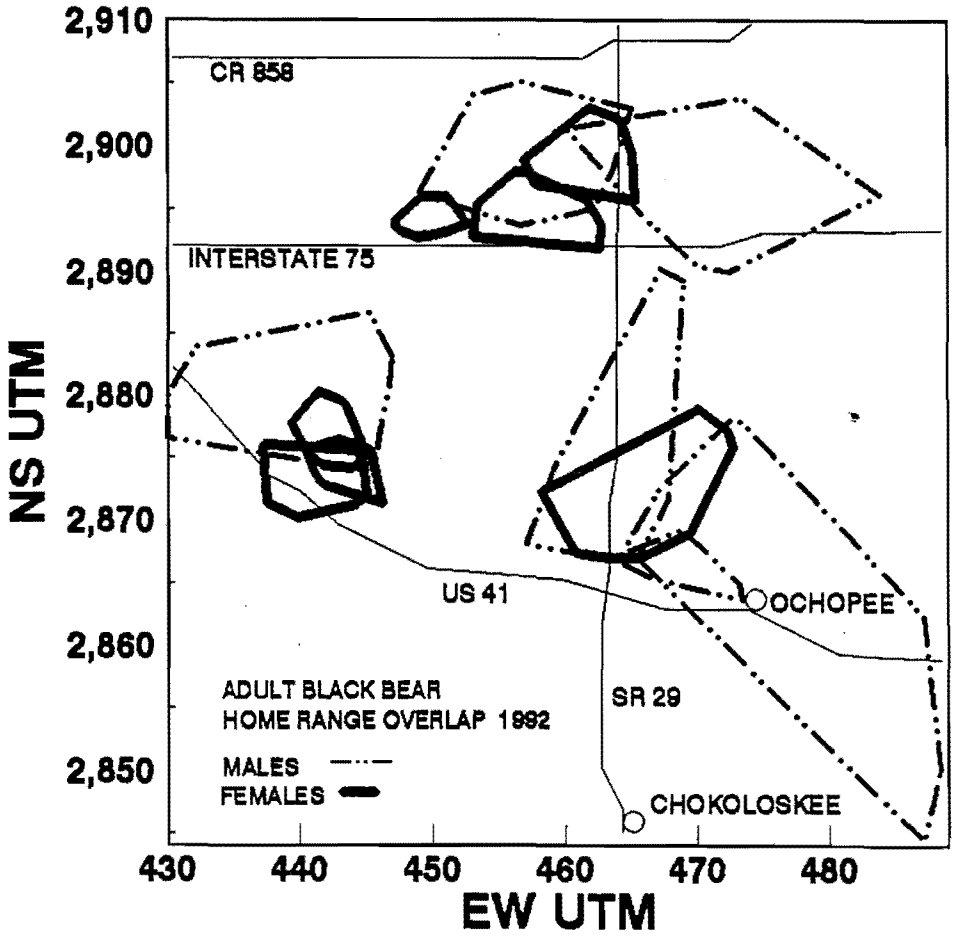


Figure 5.56. Home range overlap of resident adult black bears in southwest Florida during 1992.

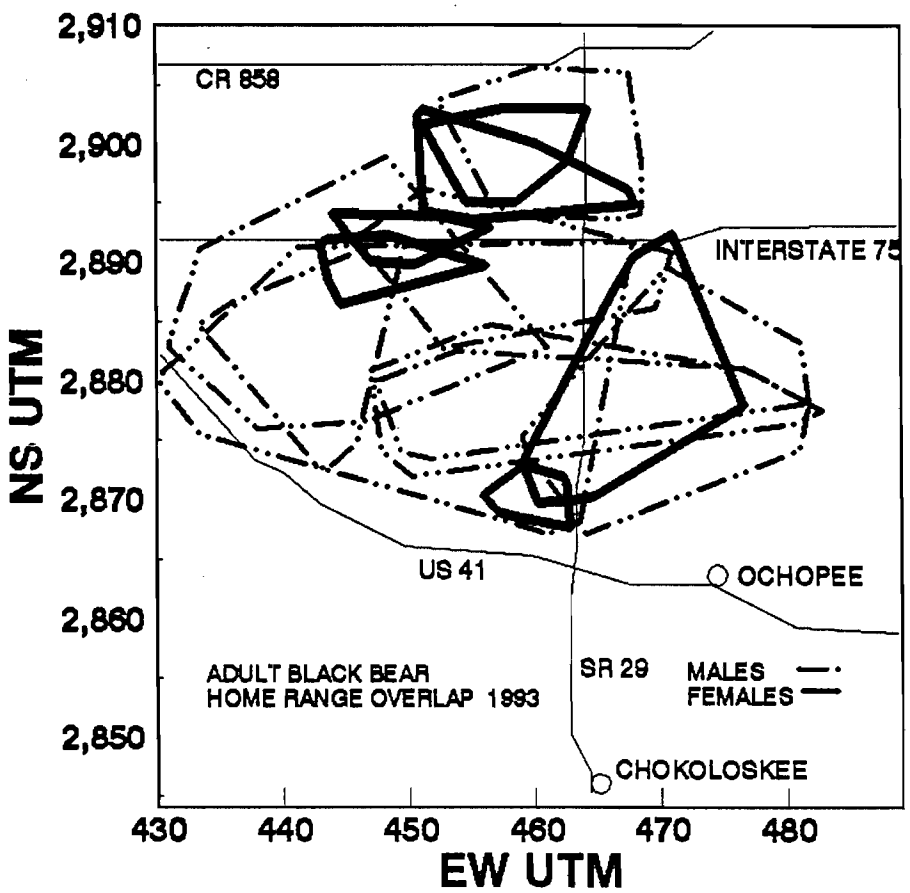


Figure 5.57. Home range overlap of resident adult black bears in southwest Florida during 1993.

thus population numbers and density were probably higher than indicated by these results. Males and females exhibited similar amounts of overlap.

Black bears routinely used woodlands close to human population centers such as Naples, Marco Island, and Ochopee; areas that panthers typically avoided. Three dispersal-aged bears (M05, M07, and M11) were captured in residential areas within front or back yards of human dwellings in Collier County. In addition, some black bear home ranges (i.e. F07, F09, M02, M13, and M18) included large areas of mangrove forest, a plant community that covers over 171,000 ha in south Florida (Odum and McIvor 1990), and was a habitat type that neither bobcats nor panthers were found to use. Although black bears and bobcats were not concurrently monitored, home ranges of most radio-collared bobcats were overlapped by several black bears in space if not in time. From a strictly spatial perspective, small winter ranges for all black bears, and denning for pregnant females and some males reduced the potential for interaction with south Florida's native cats. Given that about half of all adult females each year give birth to litters, 50% of the adult female population effectively disappears each winter. Thus, based strictly on home range size and movement patterns, the highest likelihood for interaction between black bears and sympatric felids is during summer and fall when black bears often move widely in search of mates and food.

While black bears clearly utilized the same landscape as did panthers, temporal differences in spatial arrangement between these two species accentuated the differences caused by the distinct seasonal pulses exhibited only by bears. Maehr et al. (1990b) found that Florida panthers, whether solitary or tending to kittens at dens, exhibited a pattern of sinusoidal activity with crepuscular peaks. They presumed that this pattern coincided with

the well-documented activity tendencies of potential prey. Activity patterns were not determined for bobcats, however, black bears exhibited a contrast to panthers with higher activity rates throughout the day with a diurnal peak at midday (Fig. 5.58). This finding supports the idea that prey behavioral characteristics not only influence the distribution and abundance of predators (Elton 1942, Chitty 1950, Kale 1965:58) but the activity of predators as well (Powell 1982:123). As predators of sessile food sources, black bears do not need to adjust their activities temporally in order to forage efficiently. Although many of the insects that bears feed on are highly mobile as individuals, the highest concentrations of energy can be found in eggs and larvae of termites, ants, wasps, bees and beetles. Adults of many colonial insects are diurnally active and provide visual and chemical cues to the presence of their nests which provide high energy rewards. These behavioral tendencies may encourage diurnal activity in black bears. Hourly measurements collected at automated data processing stations indicated that free-ranging black bears without cubs (n=6, 175 hours) exhibited a bimodal pattern with peaks in activity around 1100 h and 1900 h (Fig. 5.58). In addition, denning females (n=4, 339 hours) demonstrated a nearly identical pattern with activity peaks at 1100 h and 1800 h without leaving their dens. A single adult male (M08) monitored for 49 consecutive hours at his 1992 winter den showed a mid-morning activity peak with lesser increases in activity between 1400 h and 2300 h (Fig. 5.59). Comparisons of activity profiles showed that both panthers and black bears exhibit two peaks during 24 hours, however, their peaks are out of phase with each other. Panthers are clearly crepuscular (Maehr et al. 1990b), while

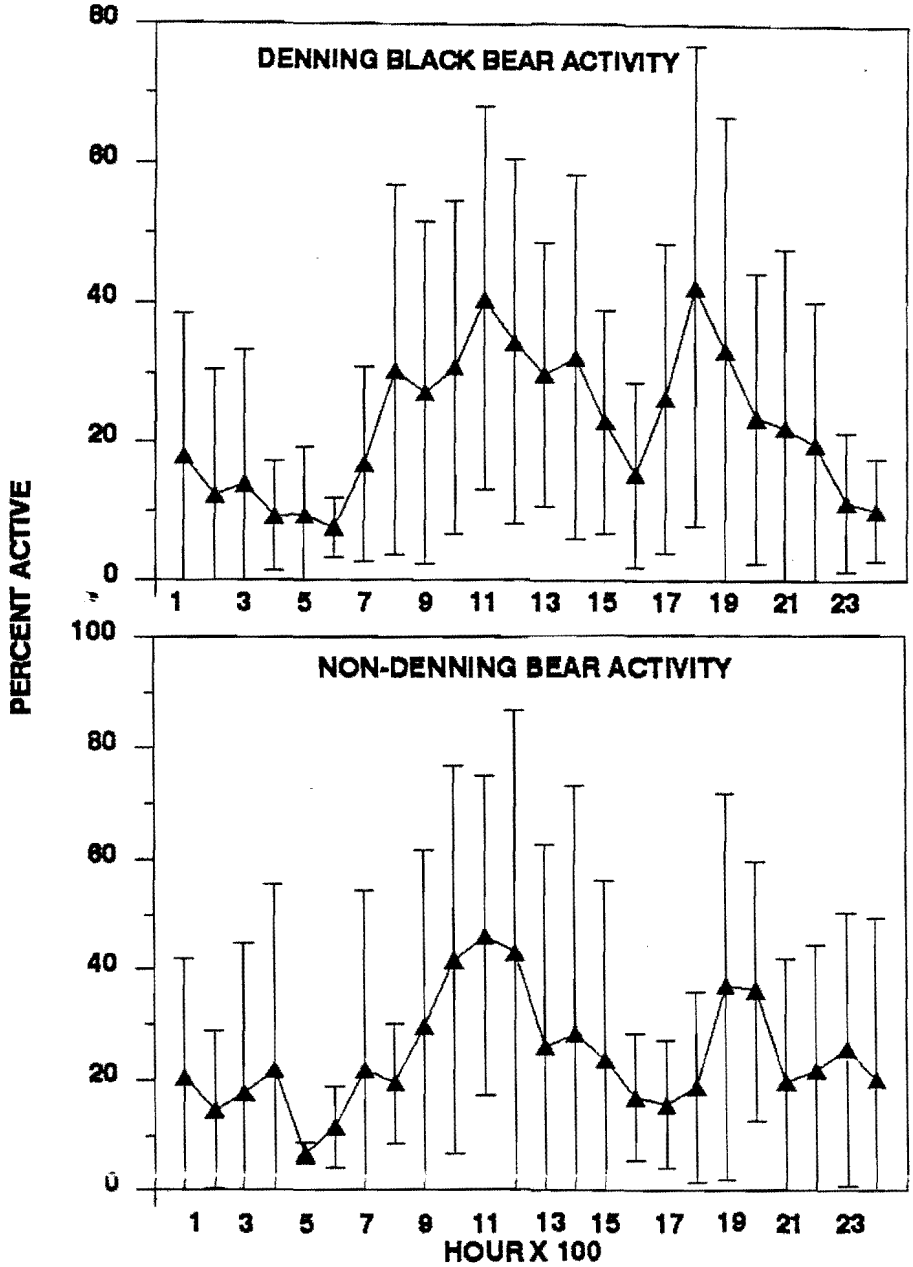


Figure 5.58. Activity of denning female black bears and non-denning black bears without cubs.

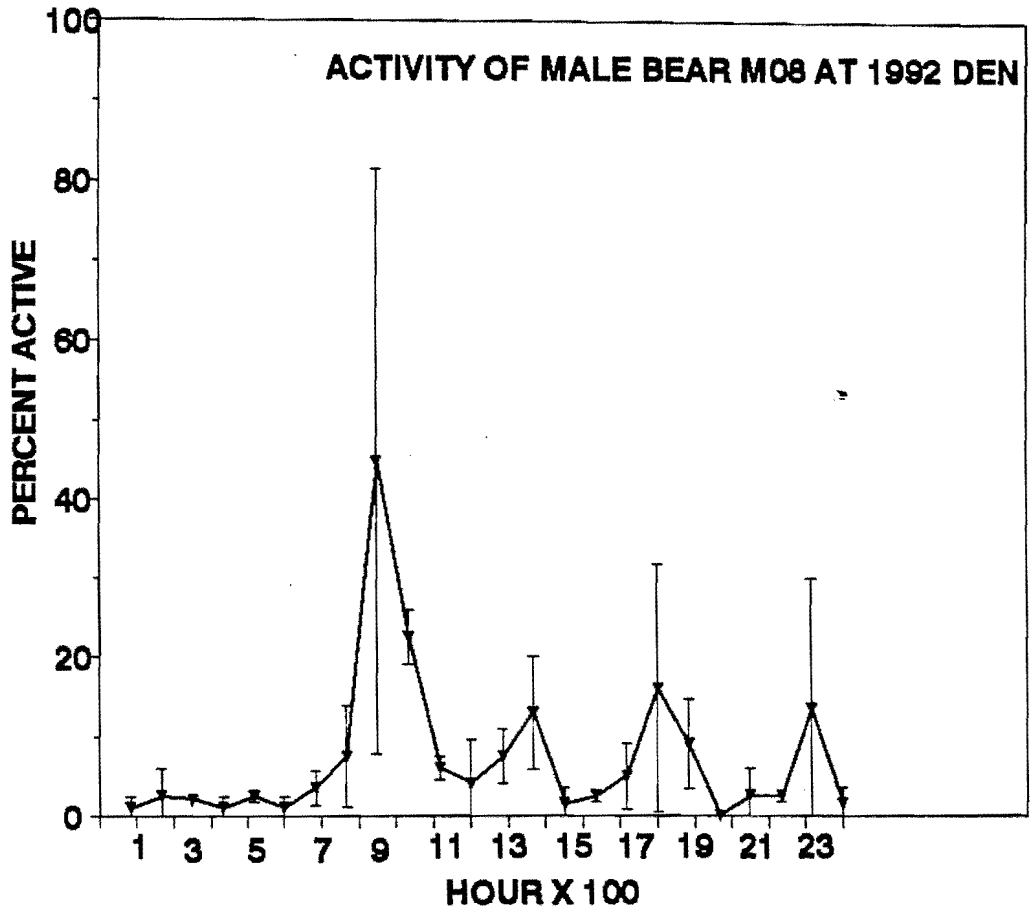


Figure 5.59. Activity during 49 continuous hours of male black bear M08 at his 1992 winter den.

black bears are diurnal with a secondary pulse of activity at or shortly after sunset. Black bears exhibited reduced activity from about 2100 h through 0800 h; the time period within which both panther activity peaks occurred.

Telemetry data and observations in the field during panther capture efforts indicated that black bears were found throughout occupied panther range. Home ranges of several bears were completely contained within larger panther home ranges (Figs. 5.60, 5.61, 5.62), whereas other bears such as those inhabiting the Fakahatchee Strand abandoned permanently occupied panther range by traveling east into Deep Lake to forage on saw palmetto fruit (Figs. 5.63, 5.64, 5.65). Given the spatial and temporal differences between black bear and panther use of a similar landscape, the likelihood for direct encounters should be minimal unless one species routinely preyed on the other. Contrasts in food habits and non-overlapping periods of daily activity of these species in south Florida suggest this is not the case.

The distinctly diurnal activity patterns of south Florida black bears reflects the limited influence of humans on their behavior. The pattern of diurnal activity in south Florida black bears coincides with observations of an adult female black bear in an area of relatively low human activity in northeastern Minnesota (Rogers 1987a). Similarly, black bears inhabiting remote areas of Idaho (Amstrup and Beecham 1976), and Great Smoky Mountains National Park (Eubanks 1976), and bears using natural forage in Sequoia National Park (Ayres et al. 1986) exhibited diurnal activity patterns that were comparable to activity patterns of south Florida black bears inhabiting remote or access-limited areas such as the Fakahatchee Strand and Florida Panther National Wildlife Refuge. Among

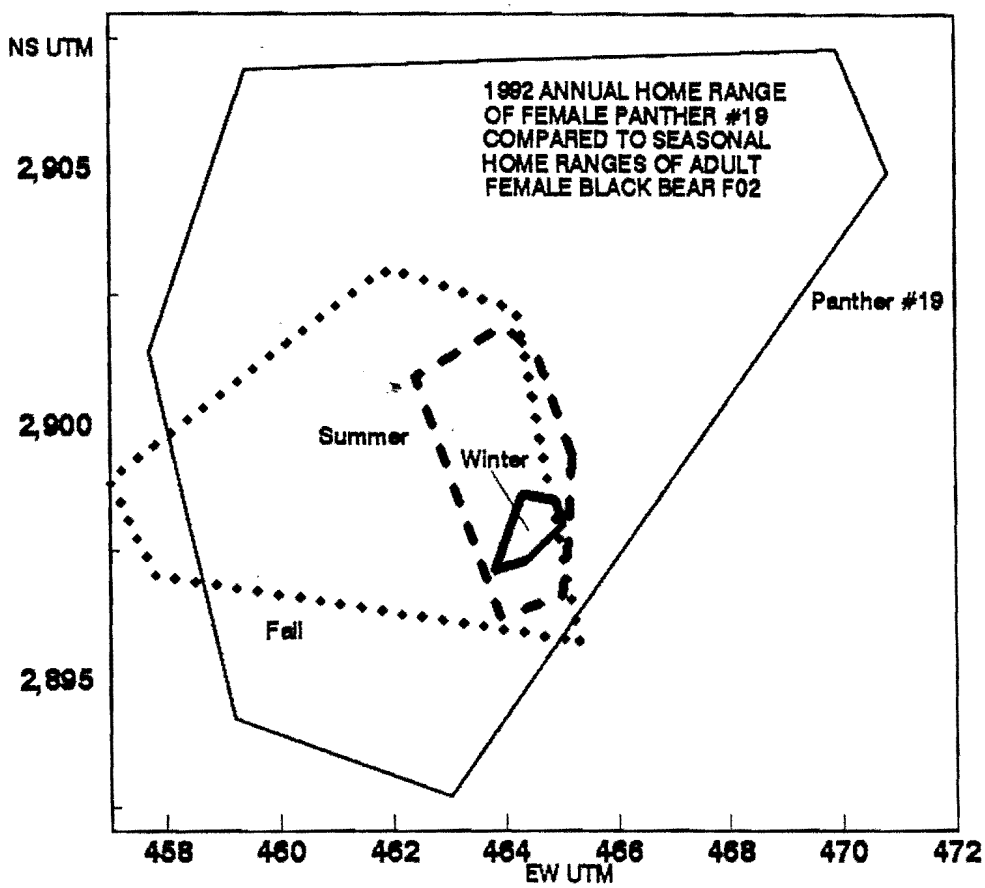


Figure 5.60. Seasonal home ranges of adult female black bear F02 compared to the 1992 annual home range of female panther #19.

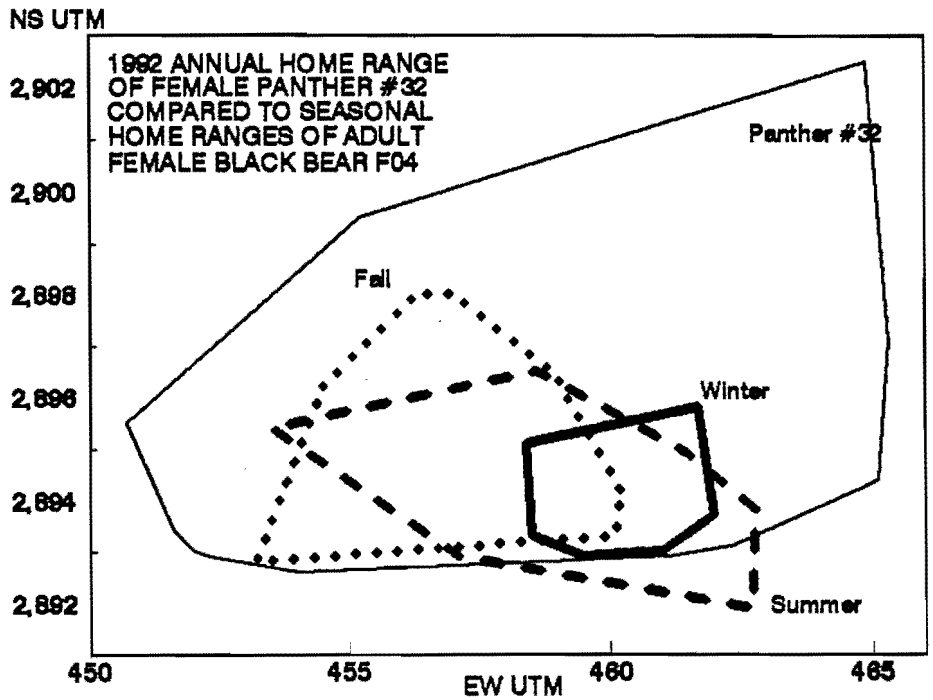


Figure 5.61. Seasonal home ranges of adult female black bear F04 compared to the 1992 annual home range of female panther #32.

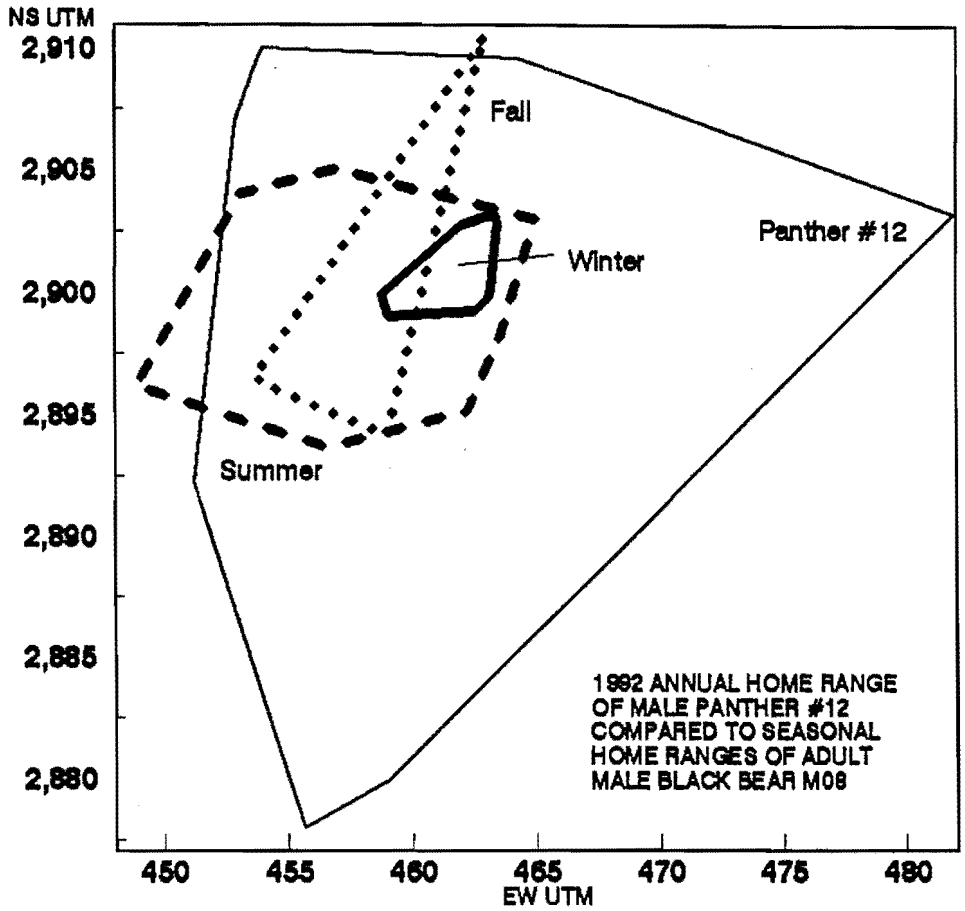


Figure 5.62. Seasonal home ranges of adult male black bear M08 compared to the 1992 annual home range of male panther #12.

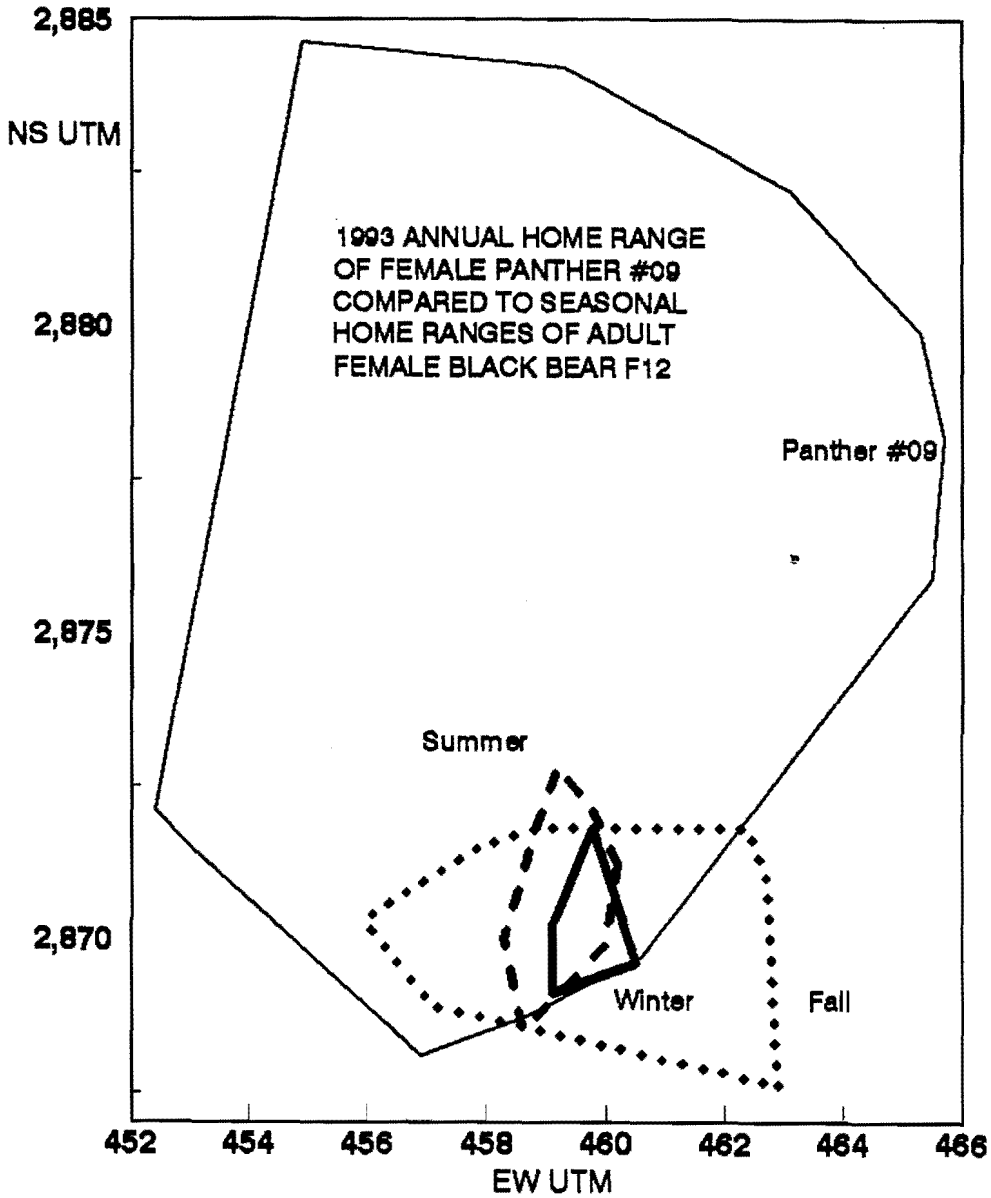


Figure 5.63. Seasonal home ranges of adult female black bear F12 compared to the 1993 annual home range of female panther #09.

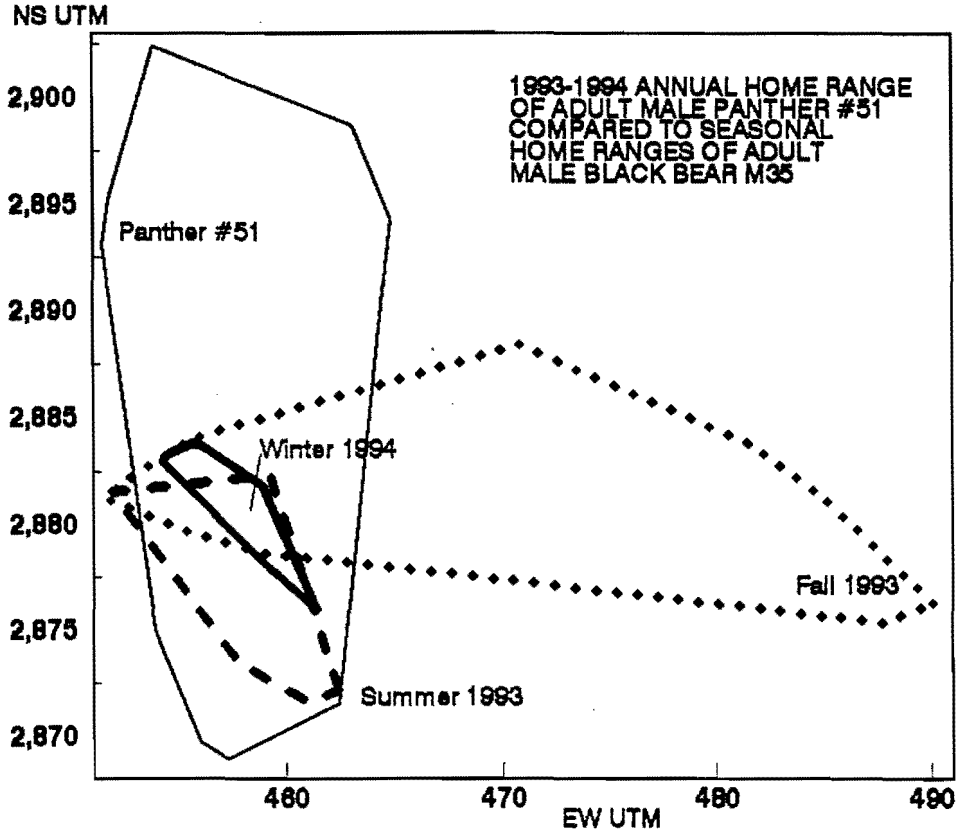


Figure 5.64. Seasonal home ranges of adult male black bear M35 compared to the 1993-1994 annual home range of male panther #51.

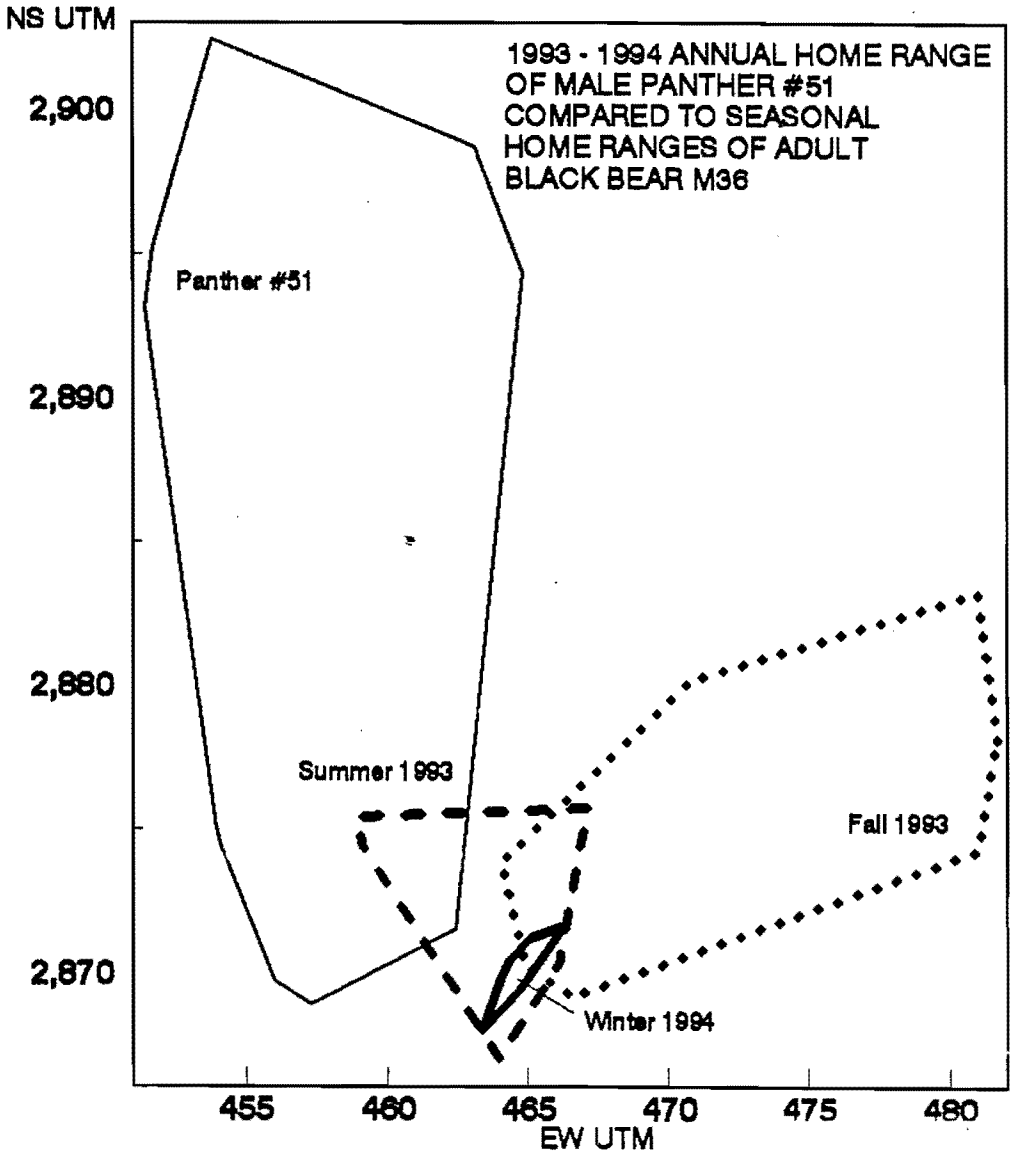


Figure 5.65. Seasonal home ranges of adult male black bear M36 compared to the 1993-1994 annual home range of male panther #51.

closely related species, Reid et al . (1991) found that Asiatic black bears (Ursus thibetanus) in remote areas of China were primarily diurnal as were giant pandas (Ailuropoda melanoleuca) in similar habitats (Schaller et al. 1989).

High levels of human activity in occupied bear range consistently shift bear activity toward nocturnality, and black bears that used foods of human origin near campgrounds were relatively inactive during daylight (Ayres et al. 1986). Among European brown bears (Ursus arctos), individuals in Italy (Roth 1983), and Spain (Clevenger et al. 1990) eschewed daytime activity in areas of moderate to high human activity. In a remote area in Yugoslavia, however, brown bears exhibited diurnal activity (Roth and Huber 1986). In North America, nocturnal activity among grizzly bears in Yellowstone National Park was attributed to visitor recreation (Gunther 1990), whereas brown bears in remote areas of Denali National Park were mostly diurnal (Stelmock and Dean 1986). Although activity of south Florida black bears inhabiting the urban-wilderness interface were not monitored in order to reveal activity patterns unique to bears at the fringe of occupied range, most complaints by local residents and beekeepers resulted from the nocturnal activities of opportunistic individuals. This suggests that south Florida black bears exhibit plasticity in temporal feeding tendencies, but where human influence is light, they exhibit the diurnal patterns expected for most undisturbed bear populations. Thus, the pattern in Florida appears to support the generality for the family Ursidae: given adequate space with appropriate resources, bears will tolerate (and in some cases take advantage of) anthropogenic dominance of the landscape.

Bobcats maintained relatively small home ranges that did not overlap with other instrumented same-sex conspecifics. Sporadic trapping efforts, however, precluded thorough sampling of even a portion of the study area, so actual densities were likely much higher than these results indicate. The findings of Wassmer et al. (1988) and Foster (1992) suggest that within forested landscapes, bobcat home ranges should be continuous with some overlap among residents. If one assumes that south Florida bobcats in 1986 and 1987 exhibited spatial patterns similar to those in south-central Florida and they were similar to bobcats studied in the same area five years later, then a single resident male panther should encompass at least 12 adult female bobcat home ranges. Overlap among bobcats and black bears should vary with season. During 1987 alone, the home range of female panther #11 overlapped with four radio-collared adult bobcats (Fig. 5.15). Bobcats were similar to bears in tolerating closer proximity to human habitations than panthers. Although none of the adults collared in this study lived adjacent to urban areas, two dispersal-age females were captured in lightly wooded residential or industrial areas east of Naples, Florida, and field sign encountered during 1987 indicated that bobcats inhabited coastal habitats surrounded by urban areas such as Pelican Bay in north Naples.

Within the forested area of Collier County that is west of County Road 951, north of U.S. Highway 41, west of State Highway 29, south of Immokalee, and north of Interstate 75 (east of State Highway 29), bobcats, black bears, and Florida panthers exhibit continuous, overlapping distributions. Outside of this area black bears inhabiting mangroves and other plant communities near the coast likely avoid potential contact with bobcats and black bears. Other zones of allopatry may occur where Florida panthers

appear to occur at low density or are absent such as in the urban areas of south Florida, the suburbanized Golden Gate Estates (north of Interstate 75), and most of the Big Cypress National Preserve and Everglades National Park where forest cover is sparse and naturally fragmented (Maehr and Cox 1995).

CHAPTER 6

DISPERSAL CHARACTERISTICS

The dispersal of subadult animals from their natal ranges is an important process that affects both population demographics and genetics (Horn 1983, Waser and Jones 1983, Shields 1987), and may determine whether or not a smaller disjunct population persists. Indeed, Horn (1983:62) observed that dispersal is "of critical importance to nearly all aspects of a species' ecology and behaviour, from the dynamics of its population to the nature of social interactions." Large carnivores typically are capable of long-distance movements that are several times greater than adult home range diameters. However, not all individuals of a particular species exhibit wide-ranging peregrinations prior to the establishment of permanent home ranges (Chepko-Sade et al. 1987). Factors such as gender, geography, population density, and human harvest are presumed to influence the frequency, distance, and success of subadult dispersers.

Forested landscapes in south Florida are fragmented by natural forces such as sloughs, lakes, and rivers that at one time were successfully negotiated by a previously more diverse carnivore community. These species exhibited semi-continuous distributions that were maintained by the movements and recruitment of individuals through a forested and rugged North American continent. An uninterrupted distribution of resident

individuals was apparently not necessary to maintain demographic linkages between disjunct breeding populations as long as they occasionally exchanged individuals. A poor understanding of species distribution and carnivore dispersal behavior may have lead to the erroneous description of Felis concolor browni, which was based on a small number of individuals that likely were occasional dispersers from populations of F. c. azteca, F. c. kaibabensis, and F. c. californica, that were traveling through poor quality desert habitat (McIvor et al. 1995). Today, the south Florida landscape contains anthropogenic barriers ranging from dredged river channels, canals and highways, to cities and expansive agricultural monocultures. These barriers are analogous to the avoided expanses of southwestern U.S. deserts, but they may also prevent south Florida carnivores from interacting with nearby populations and may block dispersing individuals from colonizing adequate but disjunct habitat far away from their natal ranges. Although it is commonly believed that free-ranging, wild-born Florida panthers are restricted to Florida south of the Caloosahatchee River, there is evidence to suggest that this may not be the case (Appendix D). Black bears have demonstrated substantial dispersal capabilities in south Florida (Maehr et al. 1988) and elsewhere (Rogers 1987a). Bobcats also exhibit long-distance dispersal capabilities (Knick and Bailey 1986, Knick 1990), but characteristics of bobcat dispersal in Florida are poorly documented. This chapter examines dispersal patterns of subadults in the south Florida carnivore community.

Methods

Study animals were monitored during regular telemetry flights. Panthers were located three times per week, black bears were located three times every two weeks, and bobcats were located approximately once per week. Location data were standardized to

account for different monitoring frequencies among species by calculating monthly arithmetic means for individual study animals. Bobcats were considered dispersers if they appeared to be young animals, were less than nine kg (Crowe 1975), and if their movements did not exhibit central tendency (Bailey 1972). Black bears were considered dispersers if cementum annuli of first premolars indicated they were less than three years of age. Dispersing panthers were captured as dependent kittens and their birth dates and independence dates known, or measurements of mass (Maehr and Moore 1992) and immature physical features such as undeveloped musculature and open epiphyses indicated they were not adults. I examined the distance between consecutive monthly mean locations, the greatest distance between radio locations, the longest distance between arithmetic means of two consecutive months, and, as an index to effective dispersal distance, the distance between the arithmetic means of first and last months of the dispersal event. Panther dispersal was considered the period following independence of kittens from their mothers to the establishment of a resident home range. Because few dependent cubs were radio instrumented and their dates of independence unknown, all subadult black bears were considered dispersers. Subadult dispersal was documented for the full duration of the event or until radio contact was lost with the study animal. For comparison, resident adult movement patterns based on monthly arithmetic mean locations were determined from one full year of telemetry data per each of four adults per species by gender groups. Analyses of variance were used to compare age and gender means between and within species for each of the four location variables. If a significant

Table 6.1. Movement characteristics of dispersal-aged Florida panthers and black bears in south Florida from 1986-1993.

Animal ID#	Months tracked	Average distance (km) between months (SD)	Longest distance between radio locations	Longest distance between consecutive months	Distance between 1st and last months
		Female black bears			
F06	19	0.9 (0.6)	9.2	1.7	0.0
F14	19	0.8 (0.5)	6.9	1.5	1.6
F15	18	0.7 (0.5)	6.4	1.9	1.5
F16	8	10.0 (15.9)	57.8	44.8	54.4
F20	9	1.2 (1.0)	7.8	3.1	1.6
		Male black bears			
M01	3	58.4 (29.3)	113.5	79.1	112.1
M10	12	4.1 (3.6)	28.1	10.3	13.9
M11	12	2.9 (3.1)	23.2	8.6	8.1
M14	9	12.3 (10.9)	66.3	27.9	4.8
M15	9	8.5 (14.0)	70.3	40.1	54.2
M16	11	12.1 (16.2)	99.2	52.9	60.0
M21	11	1.4 (0.7)	8.3	2.5	2.1
M27	12	3.7 (2.1)	21.6	8.7	9.9
M28	14	5.8 (4.2)	40.1	12.8	13.4
M32	9	4.4 (4.4)	32.7	13.3	21.4
M33	7	3.8 (3.0)	18.3	7.8	3.4
M34	11	13.0	65.1	37.8	48.5
		Female Florida panthers			
P19	21	2.5 (2.7)	23.1	11.9	9.9
P48	11	2.5 (2.3)	20.1	6.8	14.3
P52	8	3.7 (3.5)	29.1	9.8	14.0
		Male Florida panthers			
P10	3	4.4 (4.4)	23.7	7.5	7.7
P28	11	14.3 (10.4)	89.3	32.1	40.4
P29	17	7.3 (9.2)	71.5	28.2	28.3
P30	11	7.6 (6.4)	42.7	20.4	31.1
P33	9	6.0 (7.2)	38.2	22.7	32.8
P34	26	7.5 (5.7)	71.2	23.8	43.4
P43	17	10.4 (10.7)	17.9	37.5	17.2
P44	17	9.1 (19.5)	118.8	79.7	39.7
	Total	Mean (standard deviation)			
F bears	73	1.8 (5.5)	17.6 (22.5)	10.6 (19.1)	11.8 (23.8)
M bears	120	10.9 (15.5)	48.9 (33.7)	25.1 (23.2)	29.3 (33.3)
F panthers	40	2.7 (2.7)	24.1 (4.6)	9.5 (2.6)	12.7 (2.5)
M panthers	111	8.3 (3.0)	59.2 (34.7)	31.5 (21.4)	30.1 (12.3)

difference ($P<0.05$) was found, Duncan's multiple range test ($P=0.05$) was used to differentiate means.

Results and Discussion

Because only two bobcats of dispersal age were captured, the following analyses and discussion focus primarily on Florida panthers, black bears, and adult bobcats. Dispersal movements were also recorded for three female panthers, eight male panthers, five female black bears, and 12 male black bears (Table 6.1). Effective dispersal distances (distance between first and last months) ranged from 0 to 54.4 km for female black bears, 2.1 to 112.1 km for male black bears, 9.9 to 14.3 km for female panthers, and 7.7 to 43.4 km for male panthers. The longest distance between radio locations of an individual disperser was 118.8 km for male panther #44. Distances between first and last months among adults ranged from 1.1 to 3.9 km for female black bears, 2.2 to 14.9 km for male black bears, 1.1 to 5.3 km for female panthers, 0.3 to 12.3 km for male panthers, 0.6 to 2.6 km for female bobcats, and 0.8 to 2.8 for male bobcats. The longest distance between radio locations of an adult was 23.1 for male black bear M06 (Table 6.2). The longest dispersal events for bears and panthers were generally to the north and east away from urban areas (Fig.6.1).

The two dispersing female bobcats were both captured in low density suburban areas and released within 1 km of their capture sites. F11 was found dead two months after her capture, 12.9 km from her capture site in a 15.2 cm pvc pipe that acted as ventilation for a mobile home park septic system in eastern Naples, Florida. Because this was a winter "snowbird" community and no people resided here at the time of her death

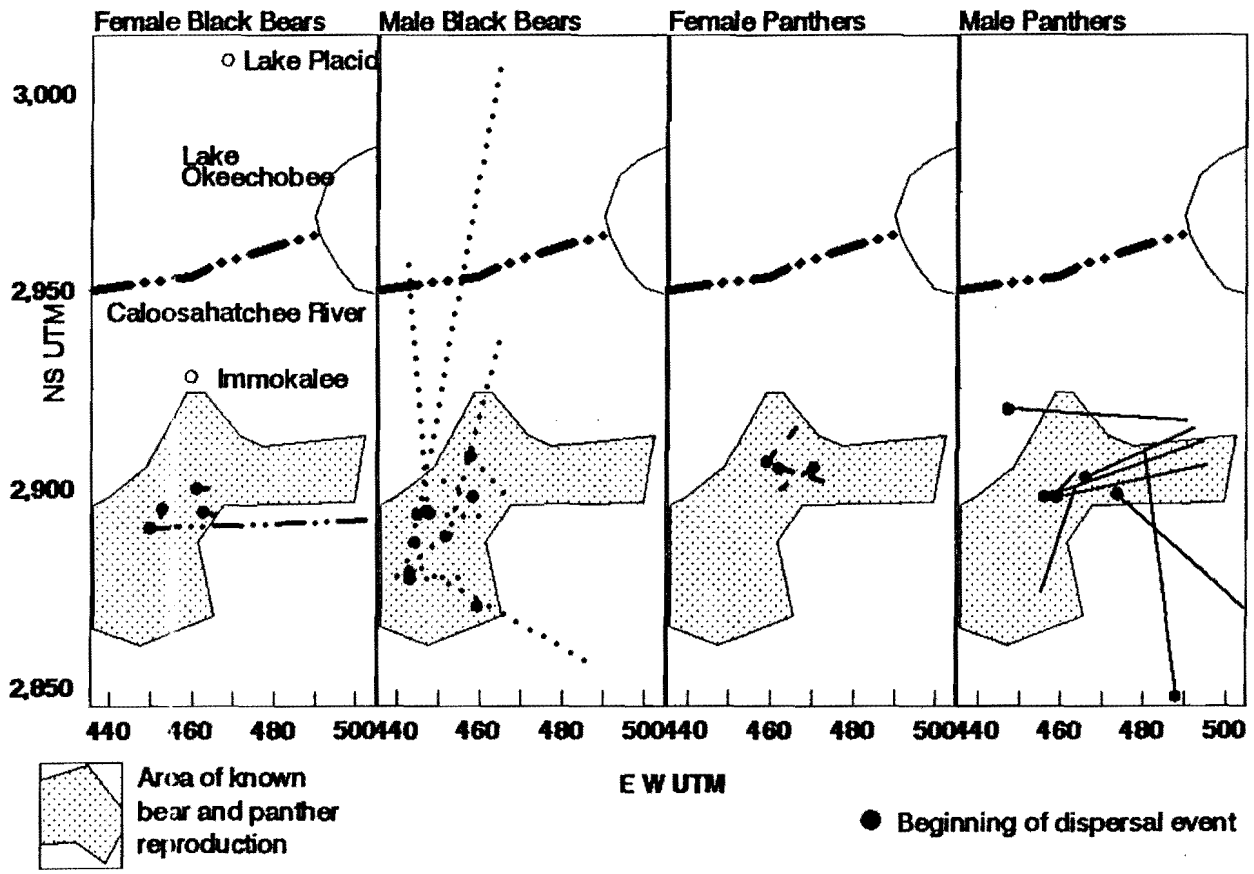


Figure 6.1. Comparison of dispersal direction and distance among male and female black bears and Florida panthers in south Florida, 1986-1993.

Table 6.2. Movement characteristics of resident adult Florida panthers, black bears, and bobcats in south Florida from 1986 to 1993.

Animal ID#	Months tracked	Average distance (km) between months (SD)	Longest distance between radio locations	Longest distance between consecutive months	Distance between 1st and last months
		Female black bears			
F04	12	1.2 (0.6)	3.8	2.1	3.9
F07	12	1.6 (0.9)	4.1	3.1	2.2
F08	12	0.7 (0.5)	2.9	1.4	1.1
F19	12	1.6 (1.1)	5.4	3.3	3.9
		Male black bears			
M03	12	5.7 (4.6)	18.0	16.4	2.2
M06	12	7.1 (5.5)	23.1	19.0	14.9
M08	12	3.7 (2.6)	13.1	9.0	9.3
M12	6	9.2 (7.5)	19.7	19.7	12.6
		Female Florida panthers			
P11	12	0.9 (0.8)	4.0	2.2	1.1
P31	12	4.1 (2.9)	12.8	8.6	2.0
P36	12	3.9 (2.8)	12.0	10.1	3.0
P40	12	2.2 (0.9)	6.1	4.1	5.3
		Male Florida panthers			
P12	12	3.9 (2.2)	13.4	7.3	7.8
P17	12	2.8 (1.8)	7.2	6.4	0.3
P37	11	4.0 (2.4)	14.0	9.7	12.3
P51	12	5.5 (2.8)	13.3	9.7	4.9
		Female bobcats			
F03	12	0.8 (0.4)	2.2	1.9	1.8
F06	9	0.9 (0.3)	2.3	1.6	1.9
F07	9	1.4 (0.9)	3.5	3.4	2.6
F09	7	0.9 (0.7)	2.1	2.2	0.6
		Male bobcats			
M01	11	1.2 (0.7)	3.6	2.6	2.8
M02	8	0.6 (0.3)	1.6	1.3	0.8
M05	6	0.9 (0.4)	2.7	1.3	2.3
M08	4	3.4 (3.7)	8.8	8.8	4.7
	Total	Mean (standard deviation)			
F bears	48	1.3 (0.4)	4.0 (1.0)	2.5 (0.9)	2.8 (1.4)
M bears	42	6.4 (2.3)	18.5 (4.2)	16.0 (4.9)	9.7 (5.5)
F panthers	48	2.8 (1.5)	8.7 (4.3)	6.2 (3.7)	2.8 (1.8)
M panthers	47	4.0 (1.1)	12.0 (3.2)	8.3 (1.7)	6.3 (5.0)
F bobcats	37	1.0 (0.3)	2.5 (0.6)	2.3 (0.8)	1.7 (0.8)
M bobcats	29	1.5 (1.3)	4.2 (3.2)	3.5 (3.6)	2.6 (1.6)

Table 6.3. Analysis of variance for movement characteristics of adult black bears, and Florida panthers in south Florida, 1986-1994. Values in parentheses are standard deviations.

Movement characteristic	Female bobcat	Male bobcat	Female bear	Male bear	Female panther	Male panther	F	P
Average distance between consecutive monthly means	1.0[1] (0.3)	1.5 (1.3)	1.3 (0.4)	6.4 (2.3)	2.8 (1.5)	4.0 (1.1)	9.7	<.001
Distance between first and last location	1.7 (0.8)	2.6 (1.6)	2.8 (1.4)	9.7 (5.5)	2.8 (1.8)	6.3 (5.0)	3.5	.021
Longest distance between two consecutive months	2.3 (0.8)	3.5 (3.6)	2.5 (0.9)	16.0 (4.9)	6.2 (3.7)	8.3 (1.7)	11.9	<.001
Longest distance between radio locations	2.5 (0.6)	4.2 (3.2)	4.0 (1.0)	18.5 (4.2)	8.7 (4.3)	12.0 3.2)	15.3	<.001

[1]Kilometers

Table 6.4. Duncan's multiple range comparisons of movement characteristics among resident adult bobcats, black bears, and Florida panthers in south Florida 1986-1994. Groupings in rows with similar letters are not significantly different (p=0.05).

Movement characteristic	Female bobcat	Male bobcat	Female bear	Male bear	Female panther	Male panther
Average distance between consecutive monthly means	1.00[1] **A**	1.52 **A**	1.29 **A**	6.41 **C**	2.80 **AB**	4.04 **B**
Distance between first and last location	1.72 **A**	2.65 **A**	2.77 **A**	9.75 **B**	2.85 **A**	6.32 **AB**
Longest distance between two consecutive months	2.27 **A**	3.50 **A**	2.47 **A**	16.02 **C**	6.25 **AB**	8.27 **B**
Longest distance between radio locations	2.52 **A**	4.17 **AB**	4.05 **AB**	18.47 **D**	8.72 **BC**	11.97 **C**

[1]Kilometers

Table 6.5. Analysis of variance for movement characteristics of dispersal-aged black bears, and Florida panthers in south Florida, 1986-1994. Values in parentheses are standard deviations.

Movement characteristic	Female bear	Male bear	Female panther	Male panther	df	F	P
Average distance between consecutive monthly means	2.72[1] (4.07)	10.87 (15.49)	2.90 (0.69)	8.32 (3.02)	3	0.91	0.45
Distance between first and last location	11.82 (23.81)	29.32 (33.27)	12.73 (2.46)	30.07 (12.27)	3	0.90	0.45
Longest distance between two consecutive months	10.60 (19.13)	25.15 (23.24)	9.50 (2.56)	31.49 (21.40)	3	1.46	0.25
Longest distance between radio locations	17.62 (22.49)	48.89 (33.69)	24.10 (4.58)	59.16 (34.7)	3	2.36	0.10

[1]Kilometers

on 6 August 1987, this appeared to be an accidental death in an anthropogenic setting. F12 dispersed 30.6 km from her capture site and was found dead of unknown causes eight months after her capture in the undeveloped southern Golden Gate Estates. Although the natal areas of these bobcats are unknown, their dispersal distances are at least four times greater than the distance between first and last locations of adult female bobcats.

Analyses of variance among species by gender groups for average distance between months indicated that adults exhibited significant differences ($F=9.7$, $p=0.001$) (Tables 6.3 and 6.4, Fig. 6.2), whereas dispersers exhibited no significant differences ($F=0.91$, $P=0.45$) (Table 6.5, Fig. 6.3). Although some dispersal-aged male bears and panthers moved long distances between months, others were relatively sedentary, and thus, high variances likely precluded the discovery of significant differences among them. Among adults, bobcat and female black bear movements were indistinguishable, male and female panther movements were similar, and male black bears moved the greatest distances from month to month.

Longest distance between two consecutive months and longest distance between radio locations were equally good at separating gender and species groupings, and created a pattern similar to average distance between consecutive monthly means (Table 6.4). The consistent pattern of differences among three out of four variables is likely the result of extensive shifts in home range location among adult male black bears, relatively large home range size among panthers, and the regular use of small home ranges among bobcats and female black bears (excluding seasonal shifts by black bears). Adult female black bears and adult bobcats feed on very different food resources, but their reproductive success is likely linked to locally abundant food supplies. Bobcats are tied to the

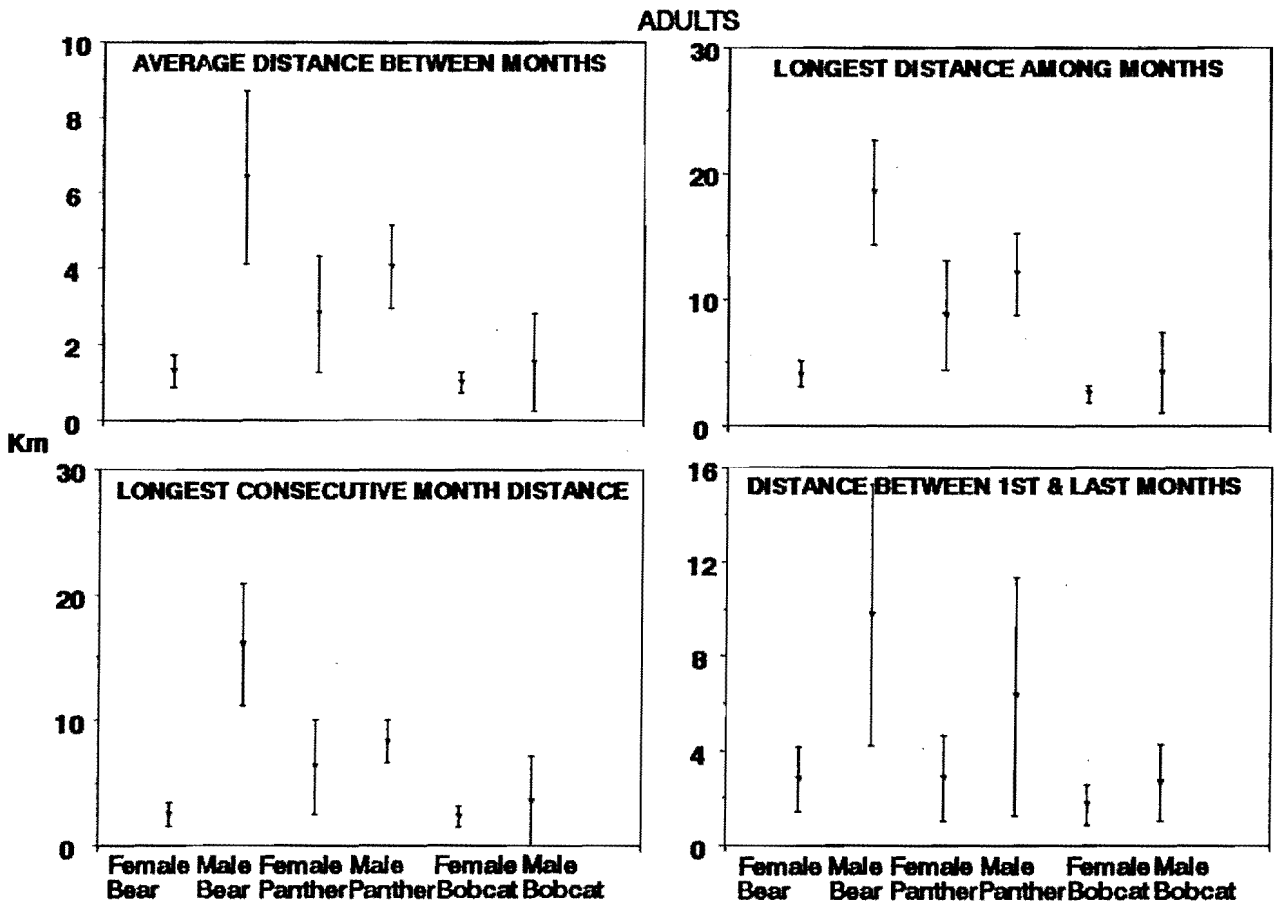


Figure 6.2. Comparison of adult black bear, bobcat, and panther movement characteristics. Vertical bars represent one standard deviation around each mean.

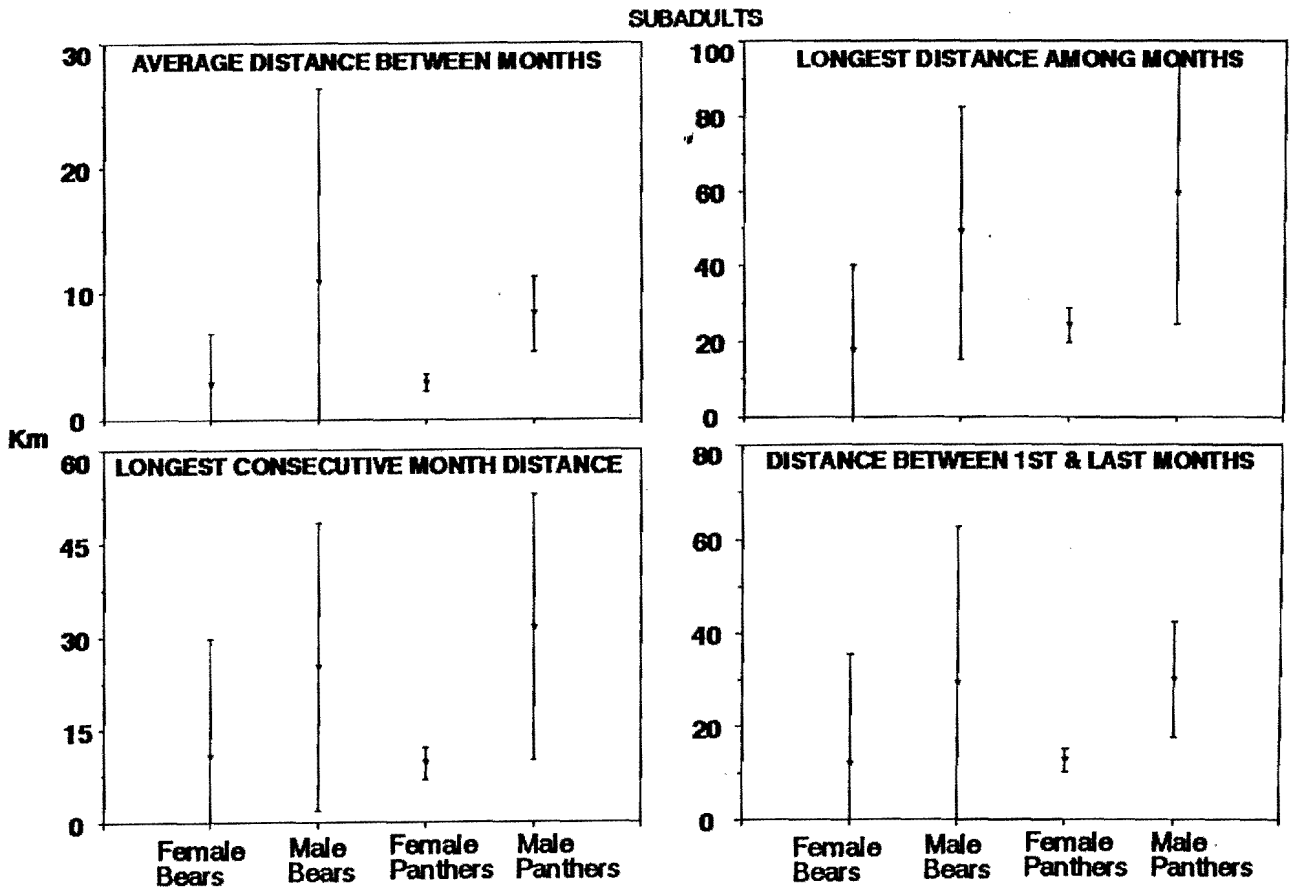


Figure 6.3. Comparison of movement characteristics among dispersal-age black bears and panthers in south Florida.

landscape largely via non-migratory small mammal prey, while female black bears require abundant plant foods in order to maintain their own nutrition as well as dependent, cubs which are relatively immobile and dependent on their mothers for approximately 18 months out of every two years. Adult male black bears are not burdened by this reproductive and nutritional anchor, and thus, are able to move widely in search of mates during summer and seek out distant food concentrations during fall. Panther prey exhibit sedentary home ranges (Land et al. 1993), but they are larger and more widely distributed than bobcat prey. Thus, differences in movement patterns between the two cat species in this study is largely a function of the scale with which they sampled the landscape, and not extremes in lifestyles.

Measurements of the distance between first and last locations suggested that all adult carnivores in south Florida tended to utilize their home ranges evenly (Table 6.4), but that some differences existed (P=0.021). Only adult male panthers and adult male black bears exhibited tendencies for less predictable movement patterns. The greater difficulty (P=0.45) for distance between first and last location to differentiate among dispersal-aged bears and panthers was due to the similarity among these distances (Table 6.5). However, because their home ranges are smaller than those of panthers, black bear dispersal events are generally more effective in distancing the disperser from its natal range.

Adults and Dispersers Compared

Adult and dispersal-aged female black bears were indistinguishable across all four movement variables (Table 6.6, Fig. 6.4). However, subadult bear F16 demonstrated the capacity for female black bears to disperse widely by traveling 54.4 km from her capture

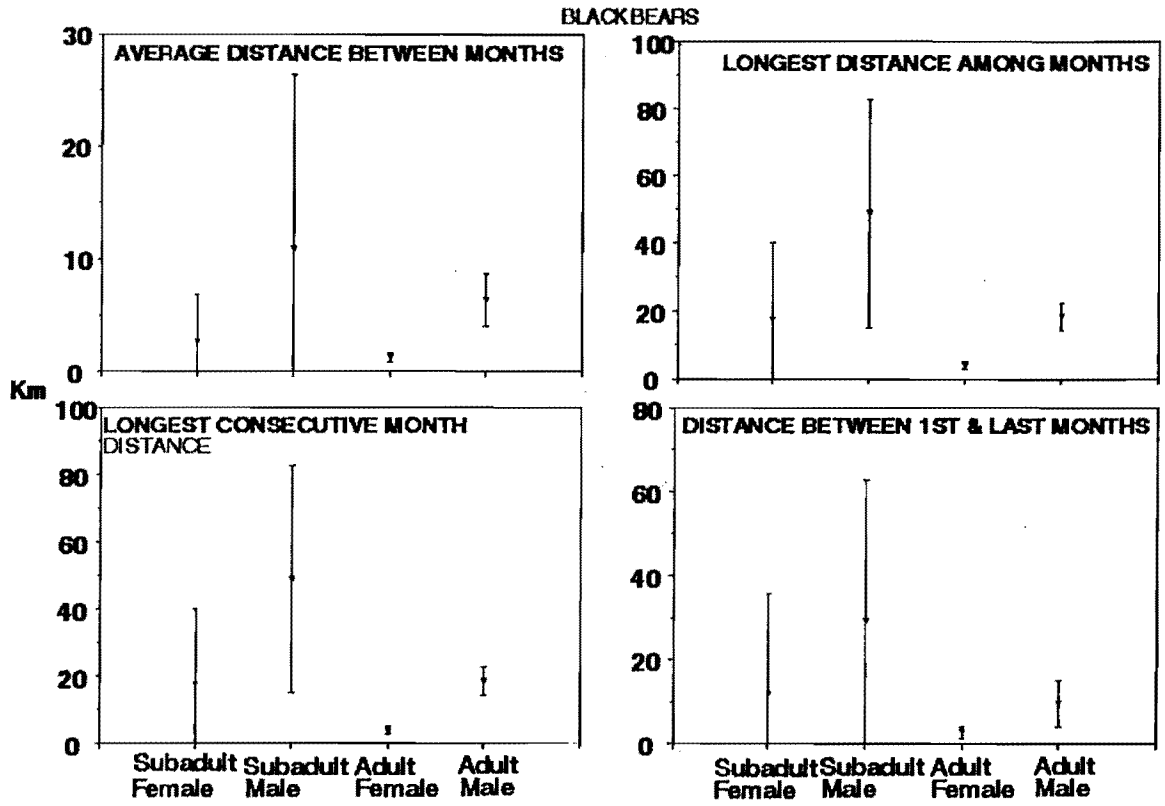


Figure 6.4. Comparison of movement characteristics among dispersal-age black bears and adult black bears in south Florida.

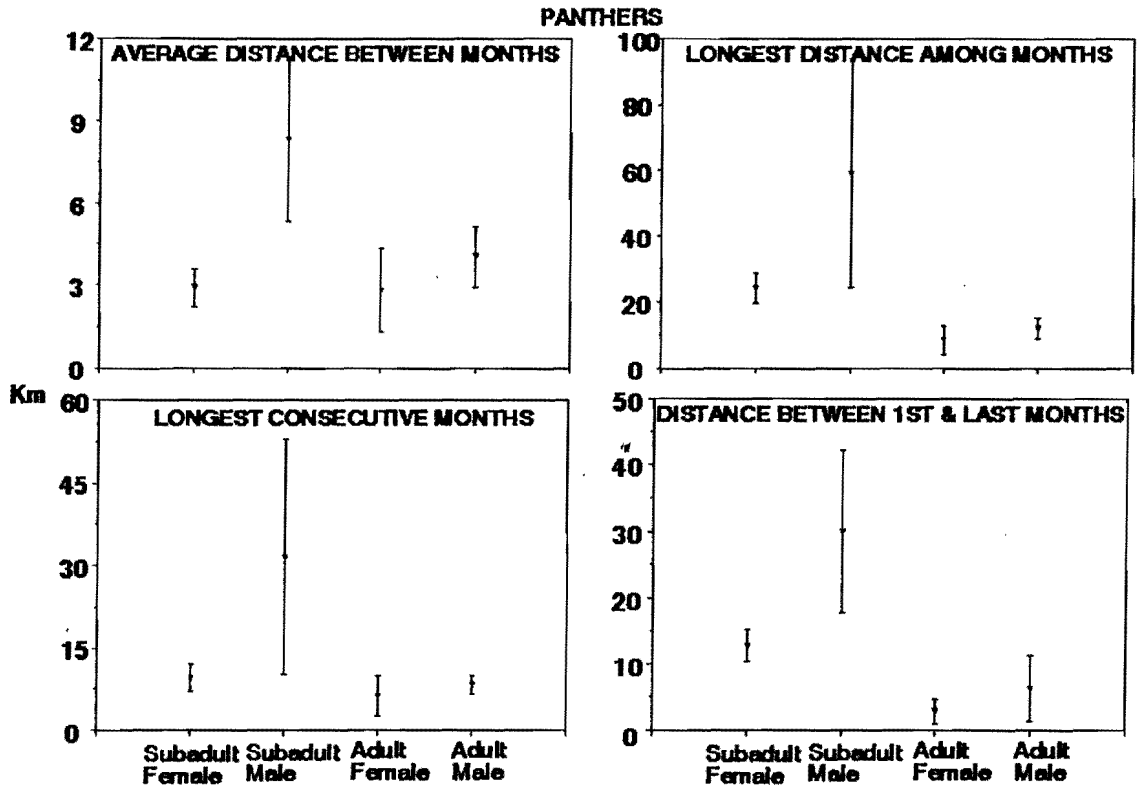


Figure 6.5. Comparis on of movement characteristics among dispersal-age panthers and adult panthers in south Florida.

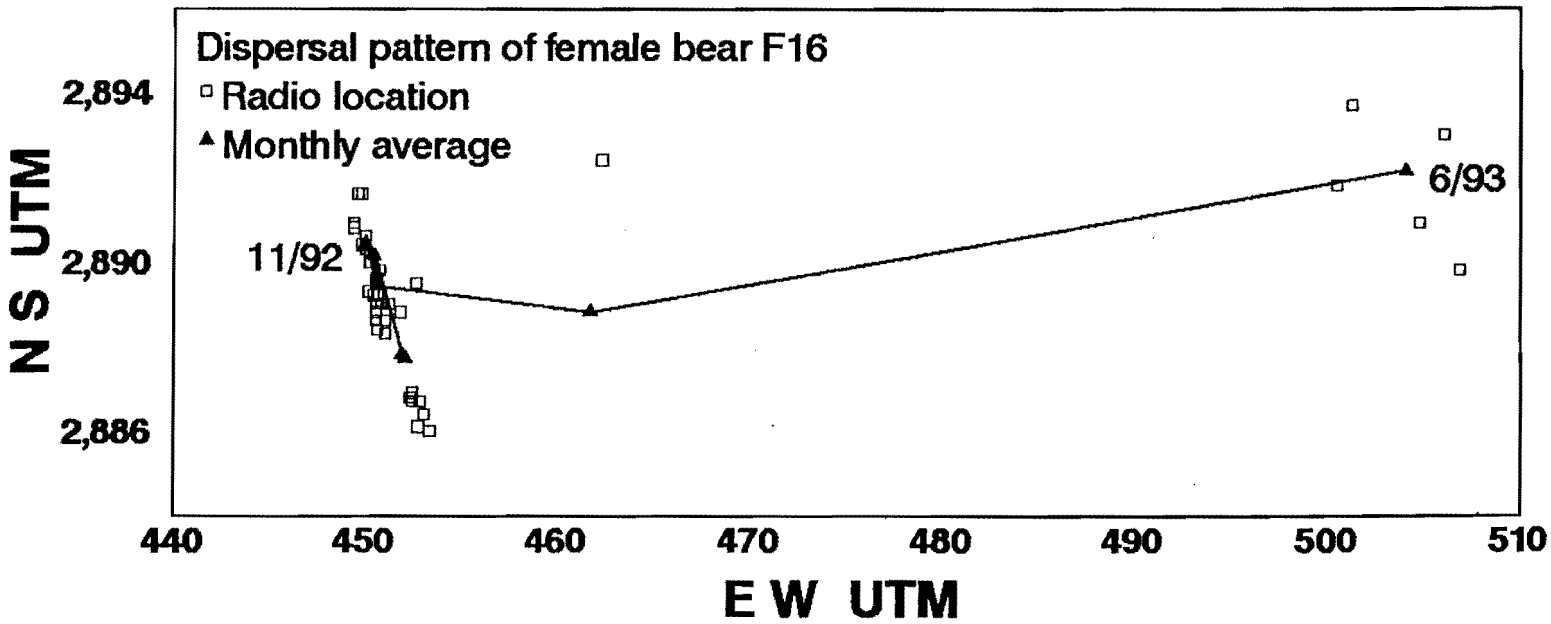


Figure 6.6. Dispersal movements of subadult female black bear F16, 1992-1993.

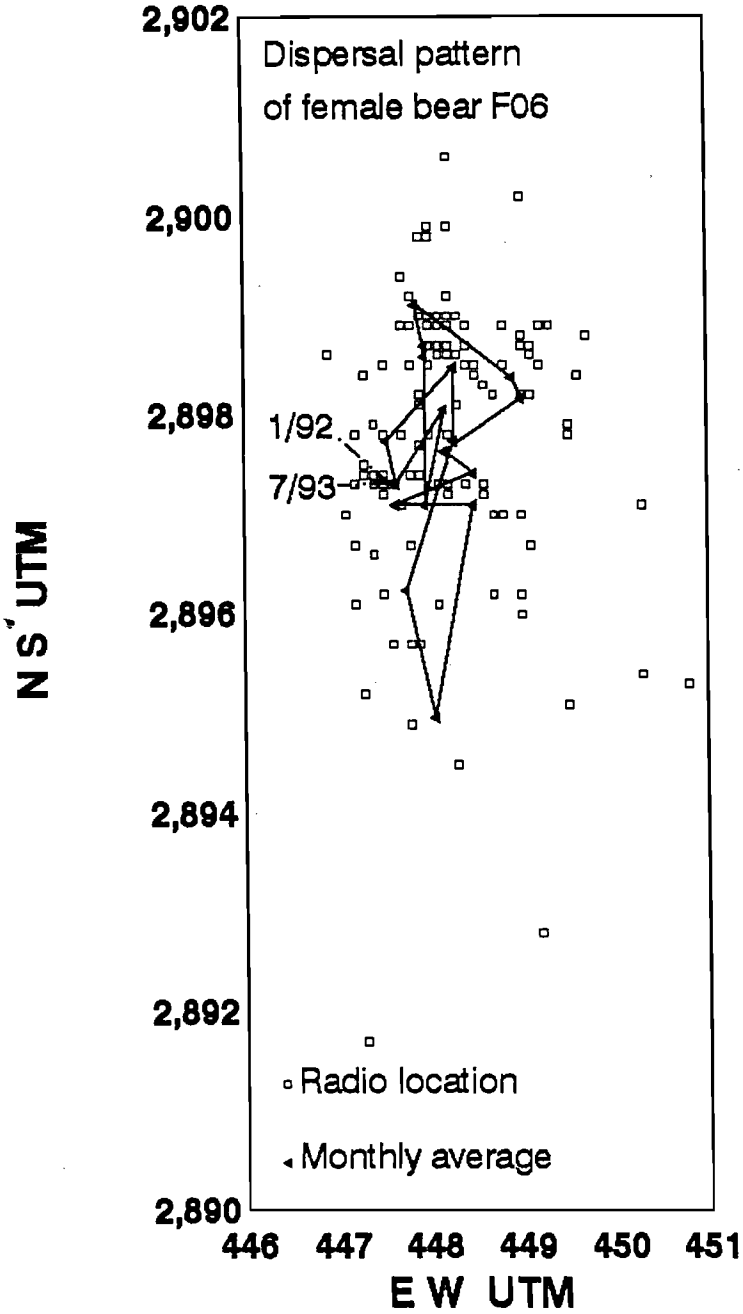


Figure 6.7. Dispersal movements of subadult female black bear F06, 1992-1993.

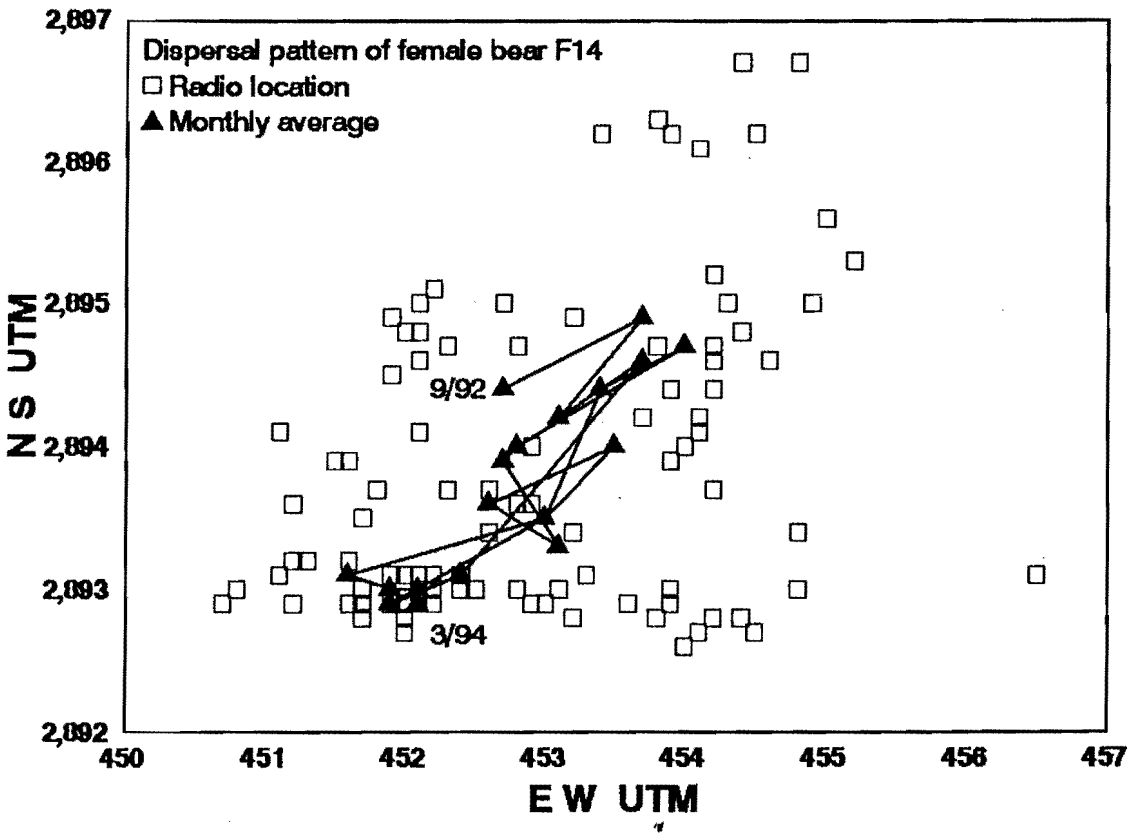


Figure 6.8. Dispersal movements of subadult female black bear F14, 1992-1994.

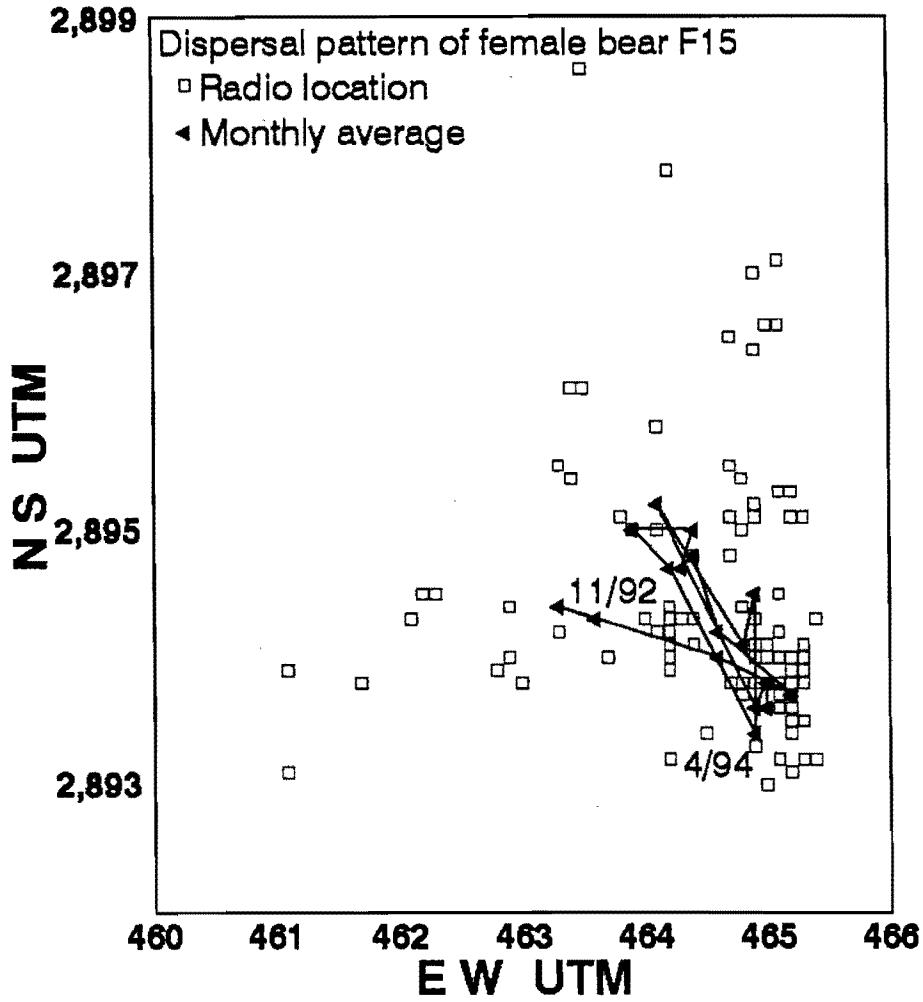


Figure 6.9. Dispersal movements of subadult female black bear F15, 1992-1994.

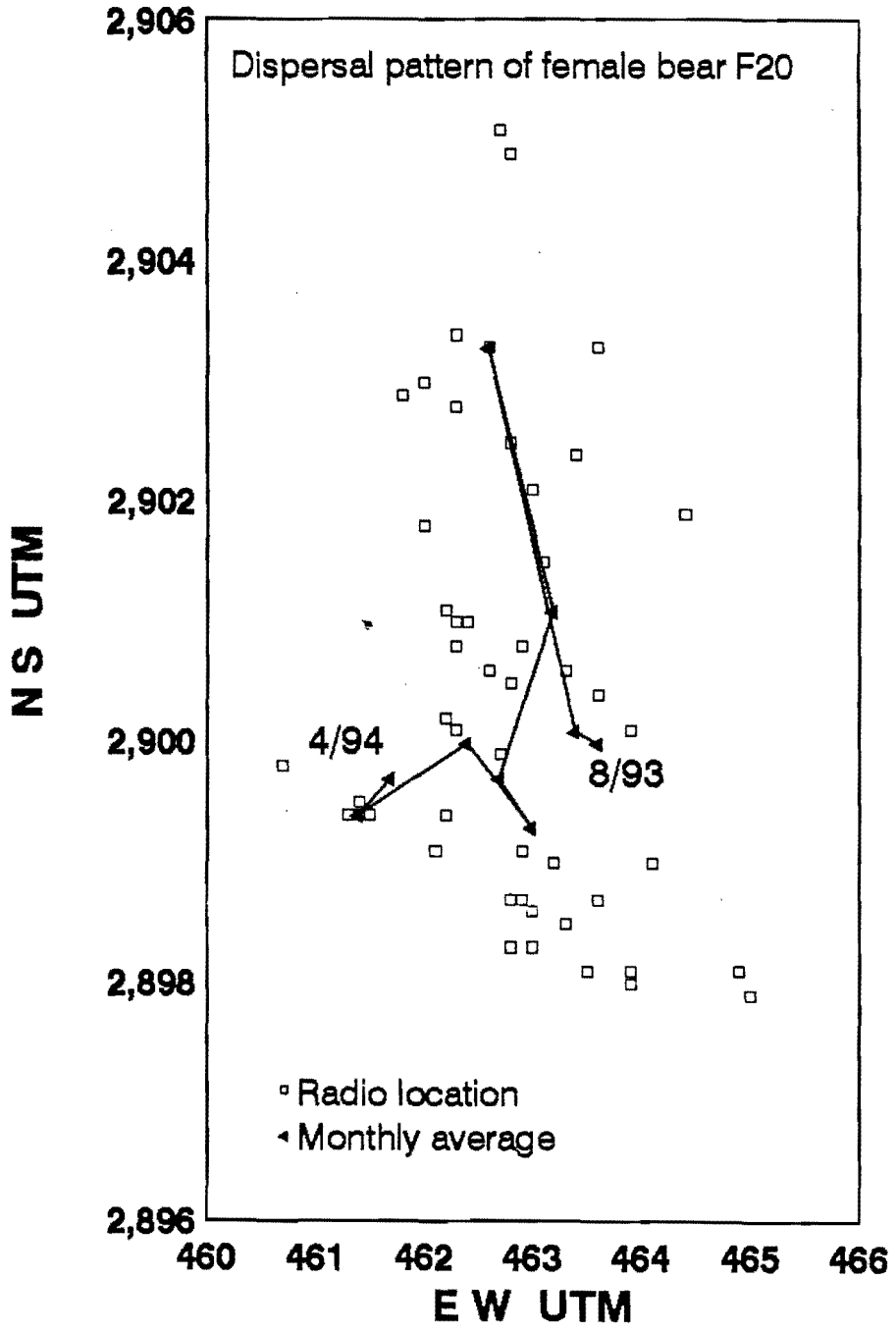


Figure 6.10. Dispersal movements of subadult female black bear F20, 1993-1994.

Table 6.6. Within species and gender analysis of variance results for comparisons of movement variables between adult and dispersing black bears and Florida panthers, 1986-1994.

Grouping	Variable	Probability of equal means	F-value
Female bears	Average distance between months	0.51	0.47
Male bears	Average distance between months	0.58	0.31
Female panthers	Average distance between months	0.92	0.01
Male panthers	Average distance between months	**0.02**	7.26
Female bears	Longest distance between radio locations	0.27	1.41
Male bears	Longest distance between radio locations	**0.03**	6.06
Female panthers	Longest distance between radio locations	**0.0002**	20.56
Male panthers	Longest distance between radio locations	**0.02**	7.02
Female bears	Longest dist. between 2 consecutive months	0.43	0.70
Male bears	Longest dist. between 2 consecutive months	0.46	0.58
Female panthers	Longest dist. between 2 consecutive months	0.25	1.66
Male panthers	Longest dist. between 2 consecutive months	**0.06**	4.47
Female bears	Distance between 1st and last radio location	0.48	0.56
Male bears	Distance between 1st and last radio location	0.27	0.27
Female panthers	Distance between 1st and last radio location	**0.0002**	38.20
Male panthers	Distance between 1st and last radio location	**0.004**	13.30

location (Fig. 6.6). The other four female black bears engaged in occasional exploratory movements but returned to within 2 km of their starting points (Figs. 6.7,6.8,6.9, and 6.10). In contrast, subadult male panthers moved greater distances than adult males across all four variables (Fig. 6.5). Subadult female panthers traveled farther than adult females between first and last radio location, and longest distance between radio locations. Both of these measurements resulted from directional movements away from natal ranges inasmuch as no subadult female panther engaged in circular movements during dispersal (Figs. 6.11,6.12, and 6.13). All female panthers captured as kittens (n=3) dispersed short distances (<15 km) and successfully reproduced in their new home ranges. Female panther #19 dispersed from her natal range after giving birth to and raising four kittens in her mother's home range (Maehr et al 1989a). This extreme philopatric breeding event was accompanied by an early age of first reproduction (18 months) that may have been the result of local saturation in resident female home ranges, and an abundant food supply within her natal range. Females #48 and #52 differed from #19 by dispersing at earlier ages but were similar in that they both gave birth to first litters before they were two years of age. Among the three dispersal-aged female panthers, only #52 dispersed far enough to leave the home range of her father (#12).

Male panthers universally displayed return movements following natal dispersal if they were not killed by conspecifics in the process (Figs. 6.14-6.21). The tendency for subadult male panthers to 'home' is likely a function of the lack of female conspecifics in peripheral areas of poor habitat quality. Subadult male panthers #28, #29, #43, and #44 were all temporary residents in areas that lacked known resident females and that

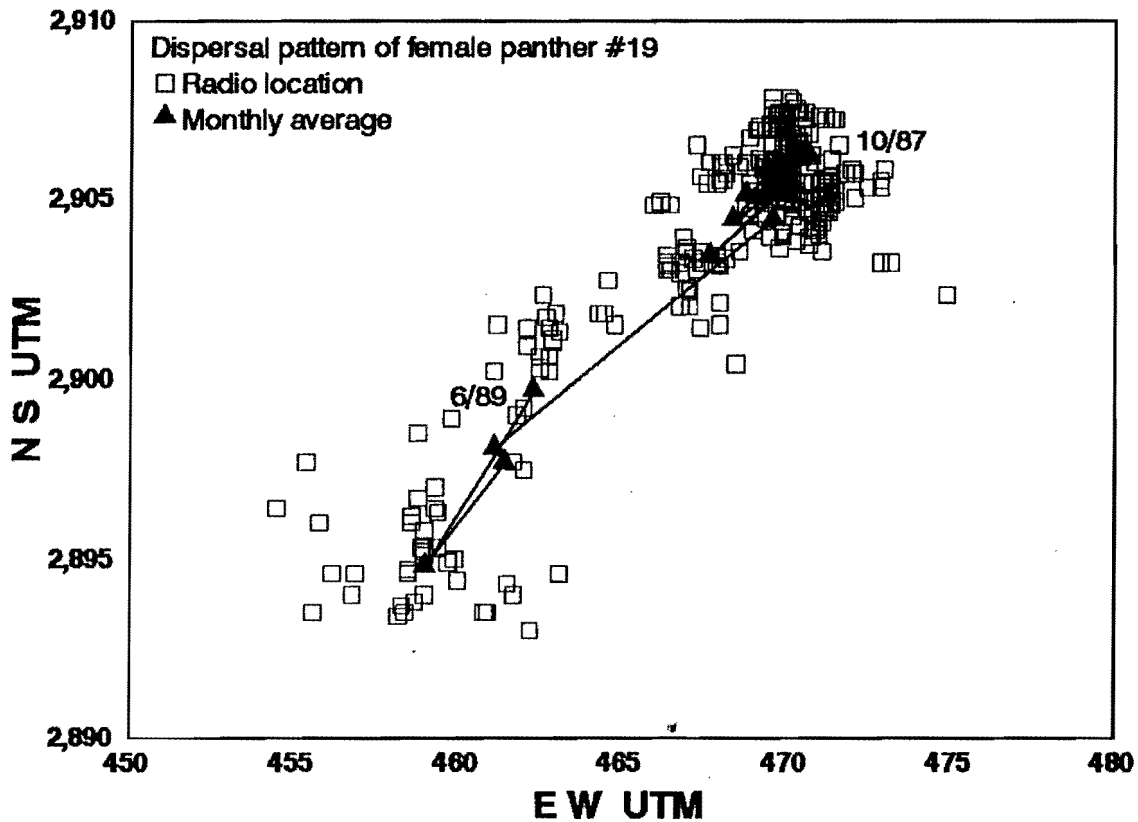


Figure 6.11. Dispersal movements of female panther #19, 1987-1989.

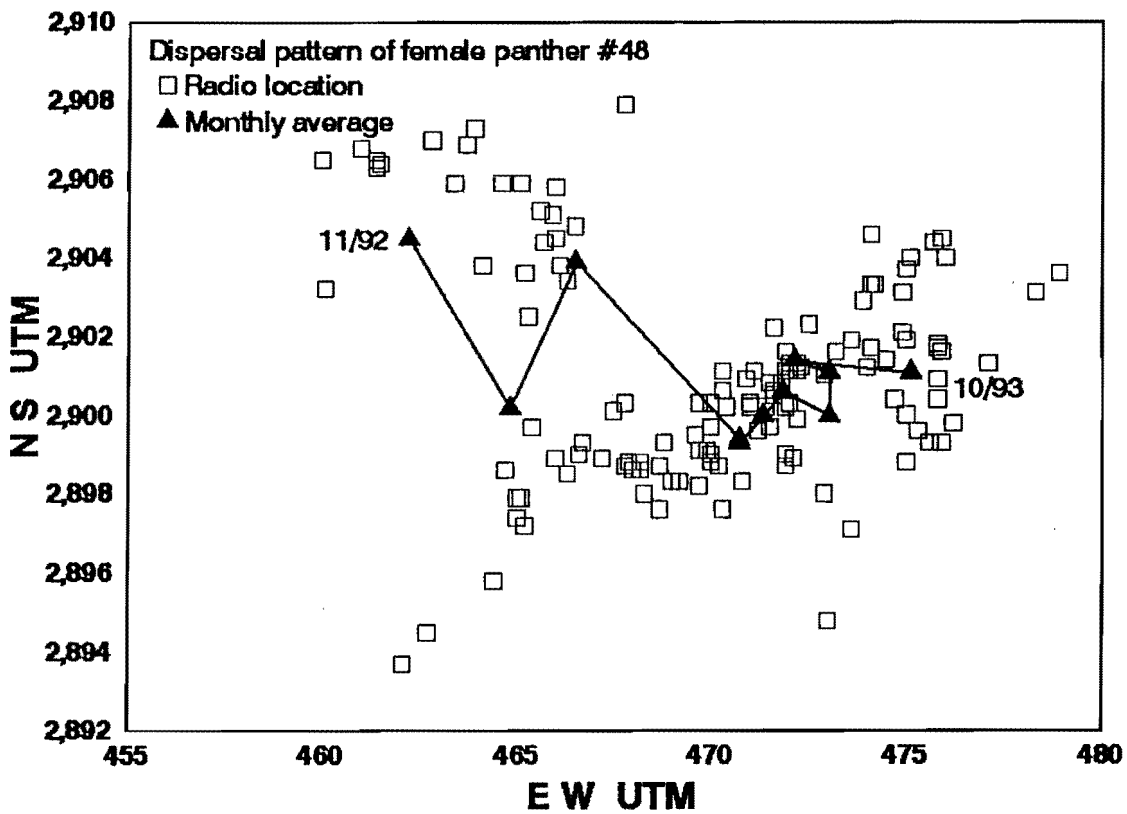


Figure 6.12. Dispersal movements of subadult female panther #48, 1992-1993.

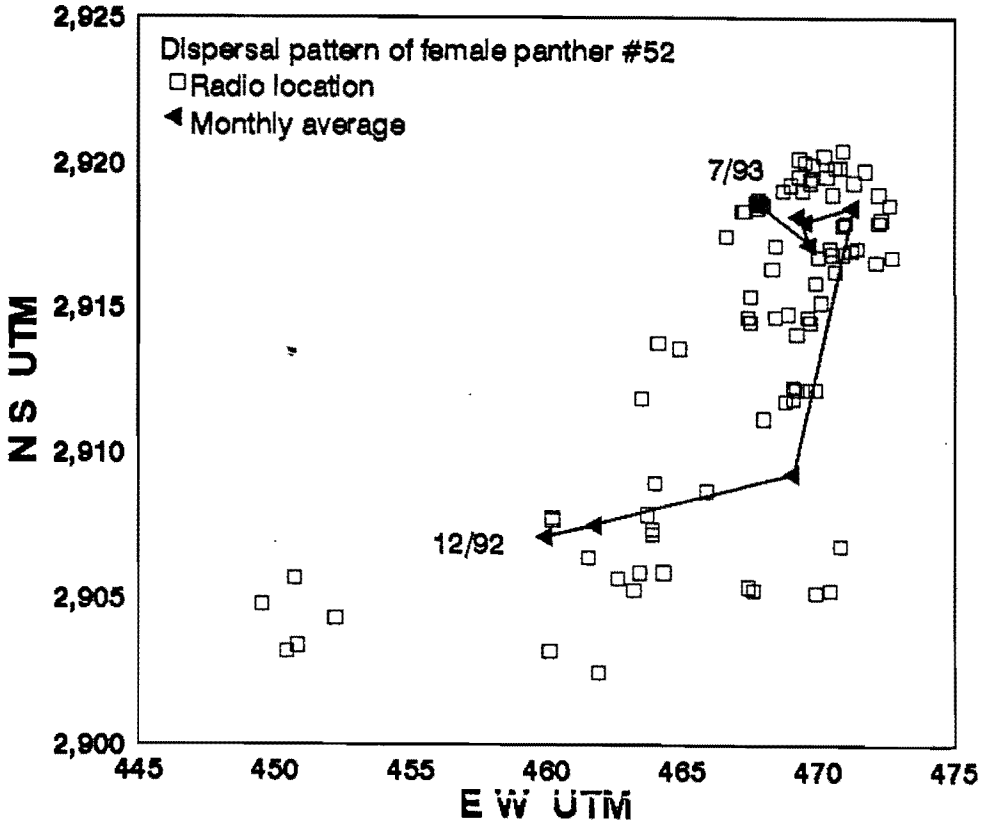


Figure 6.13. Dispersal movements of subadult female panther #52, 1992-1993.

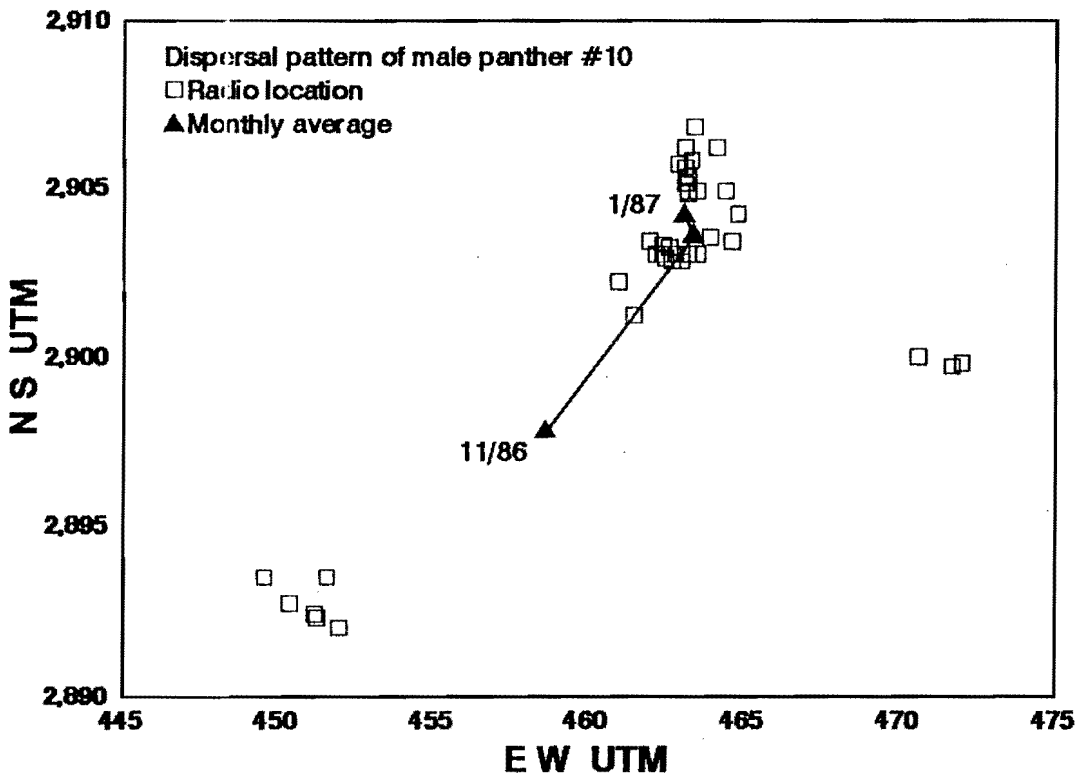


Figure 6.14. Dispersal movements of subadult male panther #10, 1986-1987.

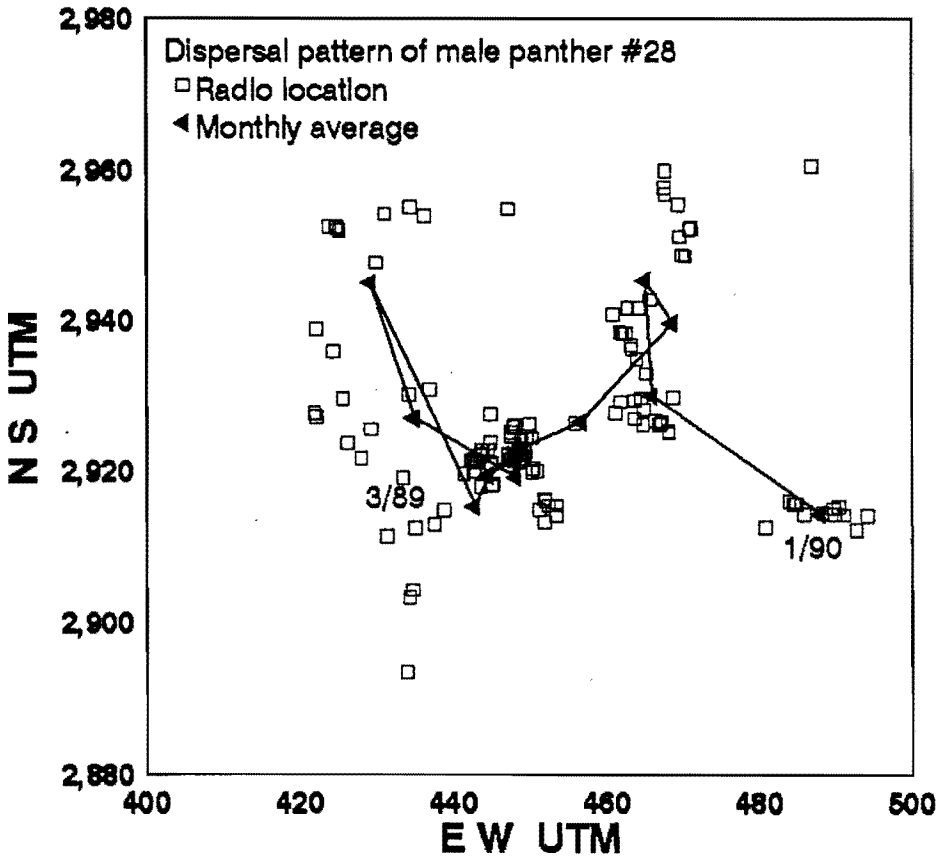


Figure 6.15. Dispersal movements of subadult male panther #28, 1989-1990.

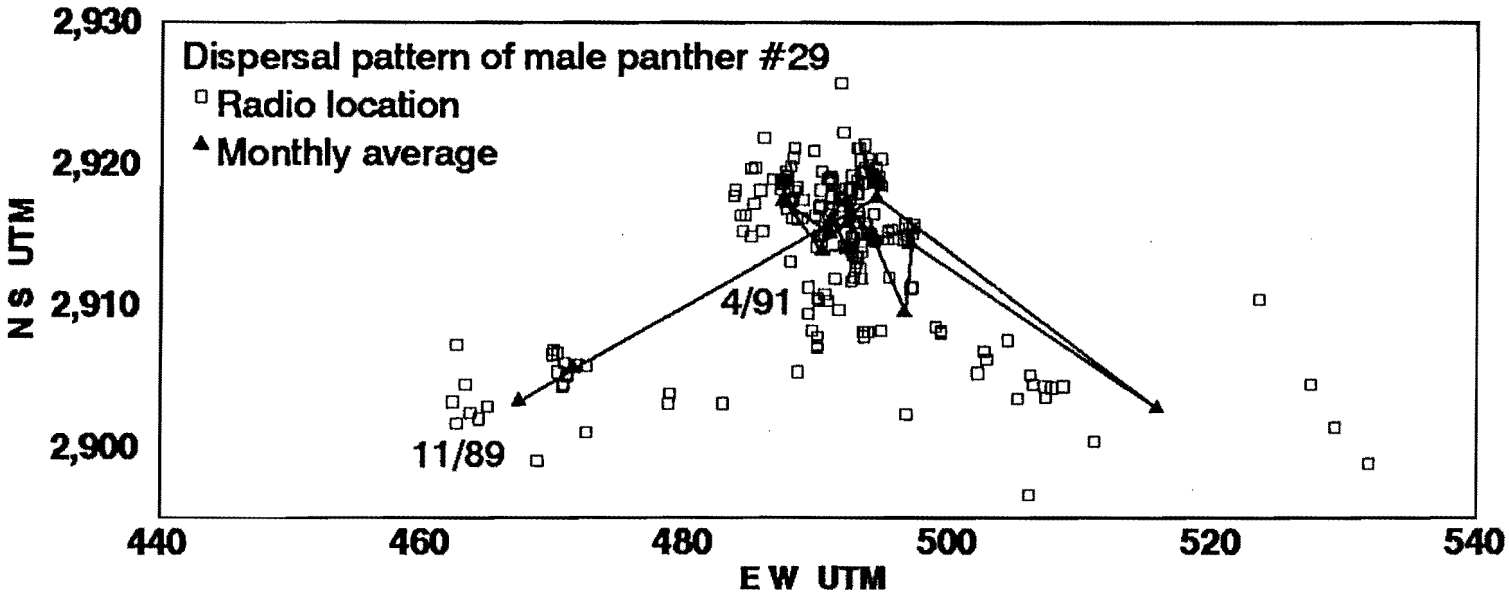


Figure 6.16. Dispersal movements of subadult male panther #29, 1989-1991.

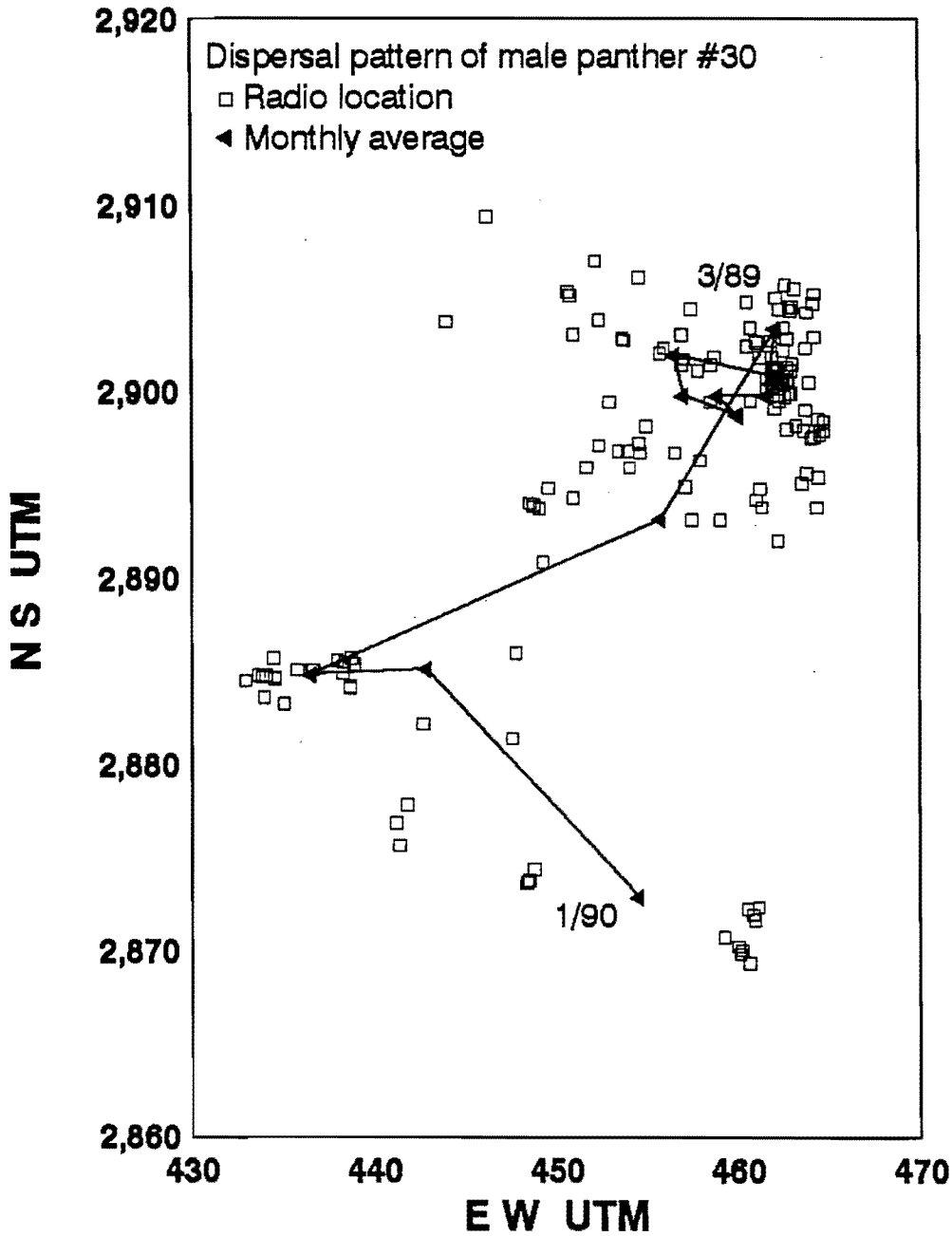


Figure 6.17. Dispersal movements of subadult male panther #30, 1989-1990.

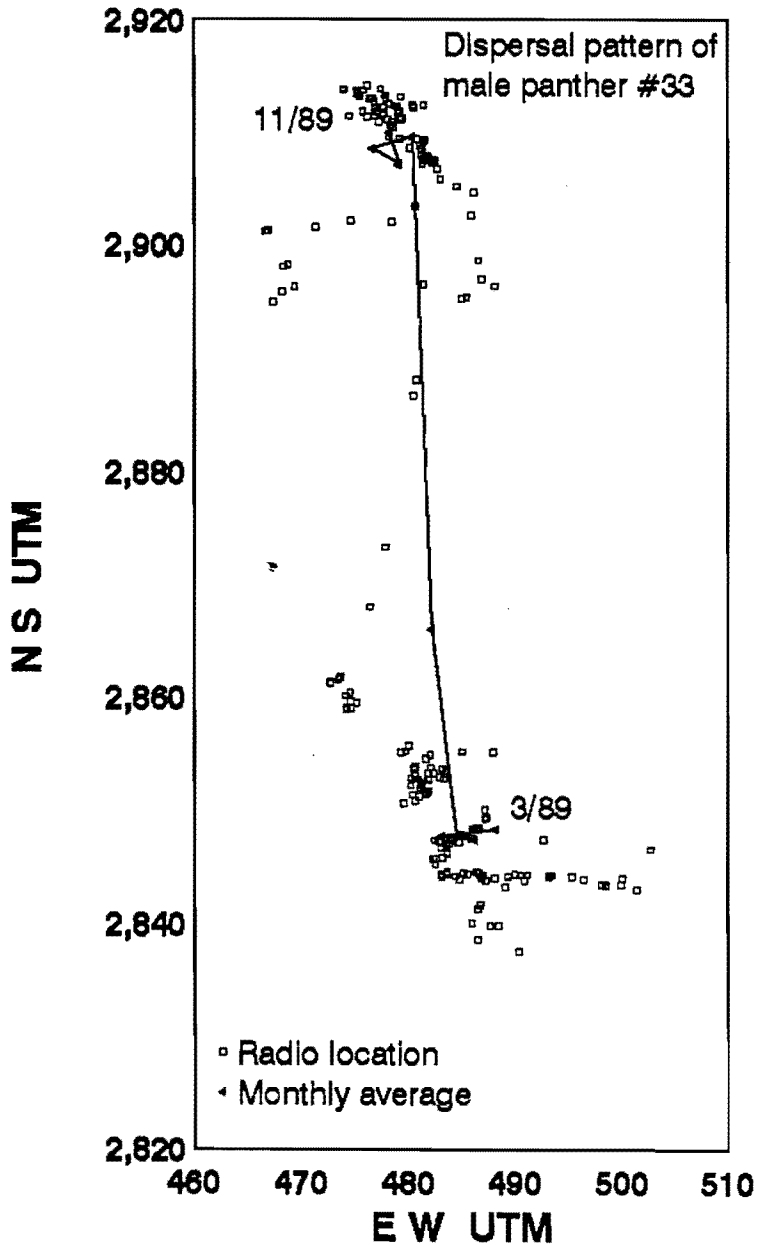


Figure 6.18. Dispersal movements of subadult male panther #33, 1989.

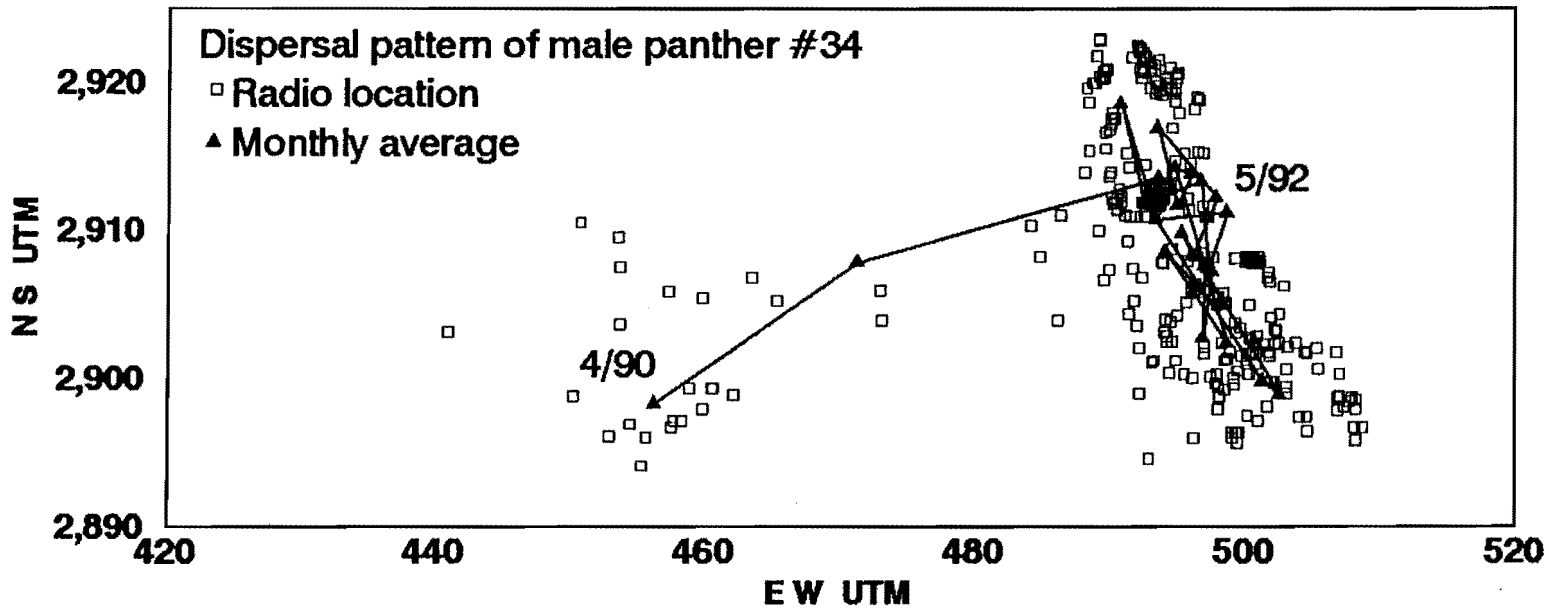


Figure 6.19. Dispersal movements of subadult male panther #34, 1990-1992.

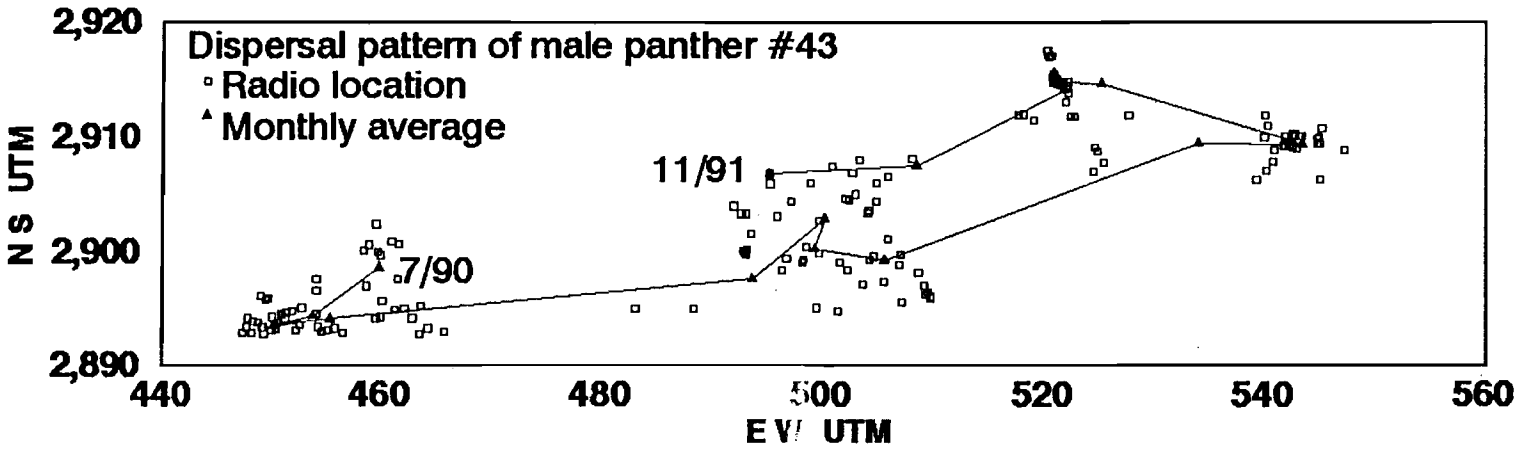


Figure 6.20. Dispersal movements of subadult male panther #43, 1990-1991.

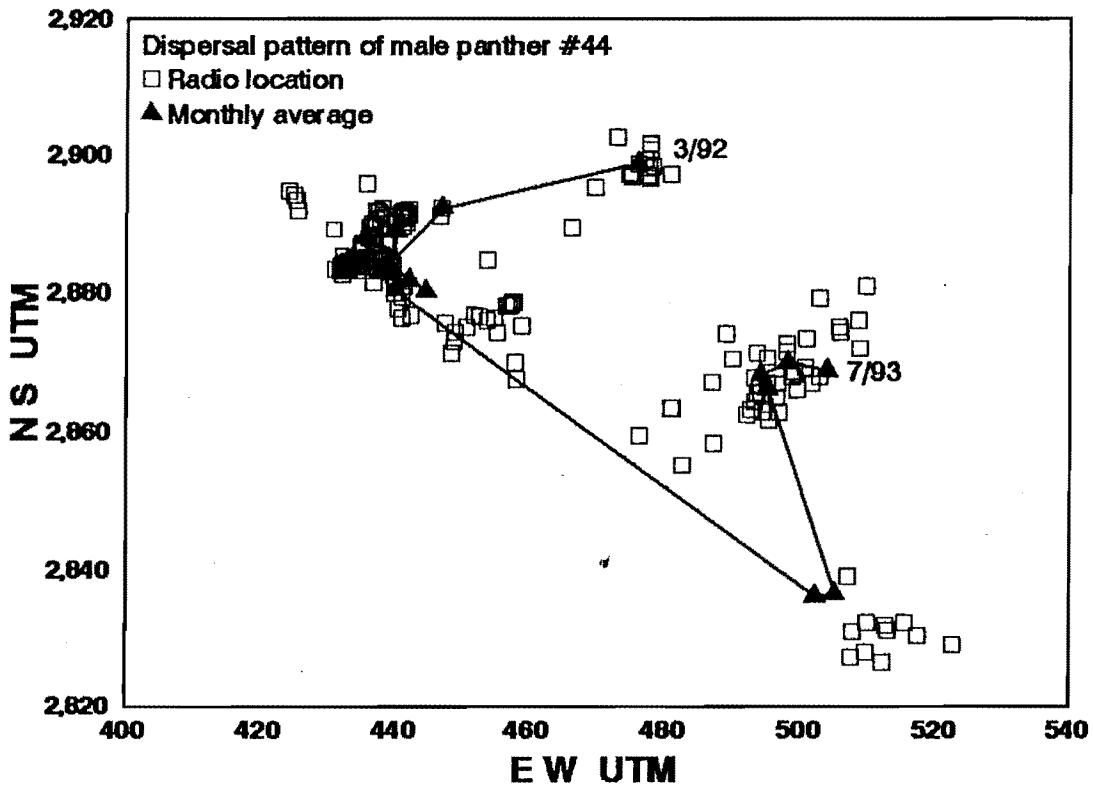


Figure 6.21. Dispersal movements of subadult male panther #44, 1992-1993.

Table 6.7. Fates of dispersing-age male panthers in south Florida, 1986-1994.

Panther ID#	Age at death (years)	Cause of death
10	1.5	Intraspecific aggression
25	4	Intraspecific aggression
28	5.5	Intraspecific aggression
29	4.0	Pseudorabies
30	1.9	Intraspecific aggression
33	3.0	Rabies
34	5.0	Bacterial infection
43	2.0	Intraspecific aggression
44	2.5	Intraspecific aggression
45	--	Alive
47	1.5	Intraspecific aggression
50	2.5	Hit by car
54	--	Alive

Table 6.8. Causes of death of resident adult male panthers in south Florida, 1984-1995.

Panther ID#	Age at death	Cause of death
01	14.0	Hit by car
02	15.0	Intraspecific aggression
04	13.0	Hit by car
06	7.0	Unknown (non-aggression)
07	10.0	Hit by car
12	14.0	Intraspecific aggression
13	8.0	Hit by car
17	9.0	Unknown
24	5.0	Unknown (non-aggression)
20	5.0	Heart failure
26	12.0	Intraspecific aggression
37	5.0	Hit by car
42	6.0	Unknown (non-aggression)

contained an abundance of avoided habitat types such as freshwater marsh, agricultural/disturbed, and urban/residential. Panthers #28 and #29 eventually established peripheral home ranges that overlapped with females but they did not sire any known litters. Among 13 subadult male panthers monitored between 1986 and 1994, 53% were killed by resident adults during dispersal (Table 6.7). In contrast, only three (23%) resident adult males are known to have died as the result of intraspecific aggression, and their ages at time of death (12, 14, and 15 years) suggest that failing health may have been a contributing factor (Table 6.8).

Black bears exhibited similar patterns of mortality susceptibility inasmuch as most deaths were attributed to dispersal-aged males. With the exception of adult male M03, documented deaths were restricted to very young and very old individuals. Out of 11 documented black bear deaths, 10 were among males and 60% of these occurred among individuals between 2.5 and 3.5 years of age (Table 6.9). However, death among radio-instrumented black bears were primarily human-caused (at least 50% by illegal killing). Only one bear (9%) was known to have been killed by a conspecific.

Although individual dispersing black bears demonstrated a greater potential to move long distances than resident adult bears (Table 6.6), the lack of significant differences between them for most distance measurements was due to high variance caused by the seasonal shifts in home range location exhibited by most adults. Subadult male bears M01 and M16 moved greater than 110 and 75 km, respectively, before the former was killed as a nuisance animal in Highlands County (see Maehr et al. 1988), and the latter experienced transmitter failure (Figs. 6.22 and 6.23). These were the only animals among the three study species that crossed the Caloosahatchee River. Further,

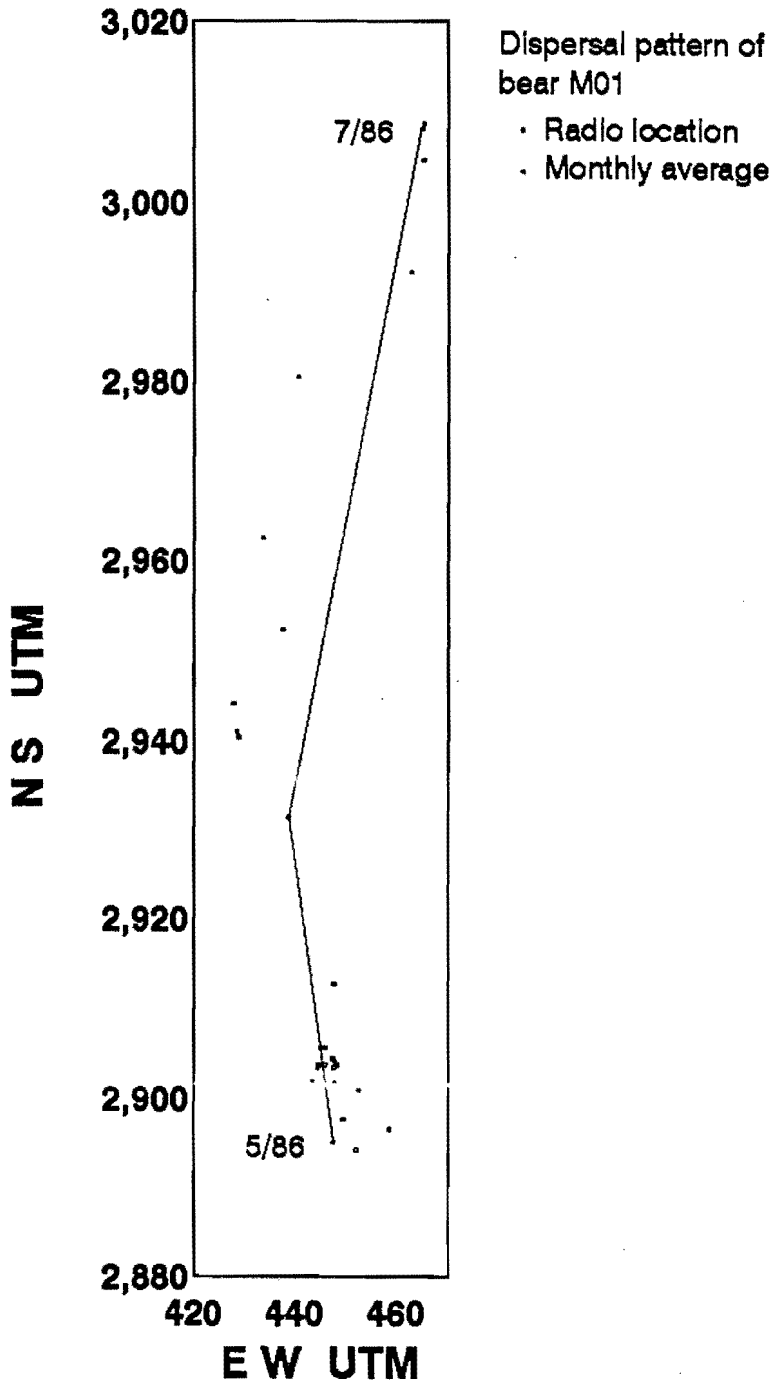


Figure 6.22. Dispersal movements of subadult male black bear M01, 1986.

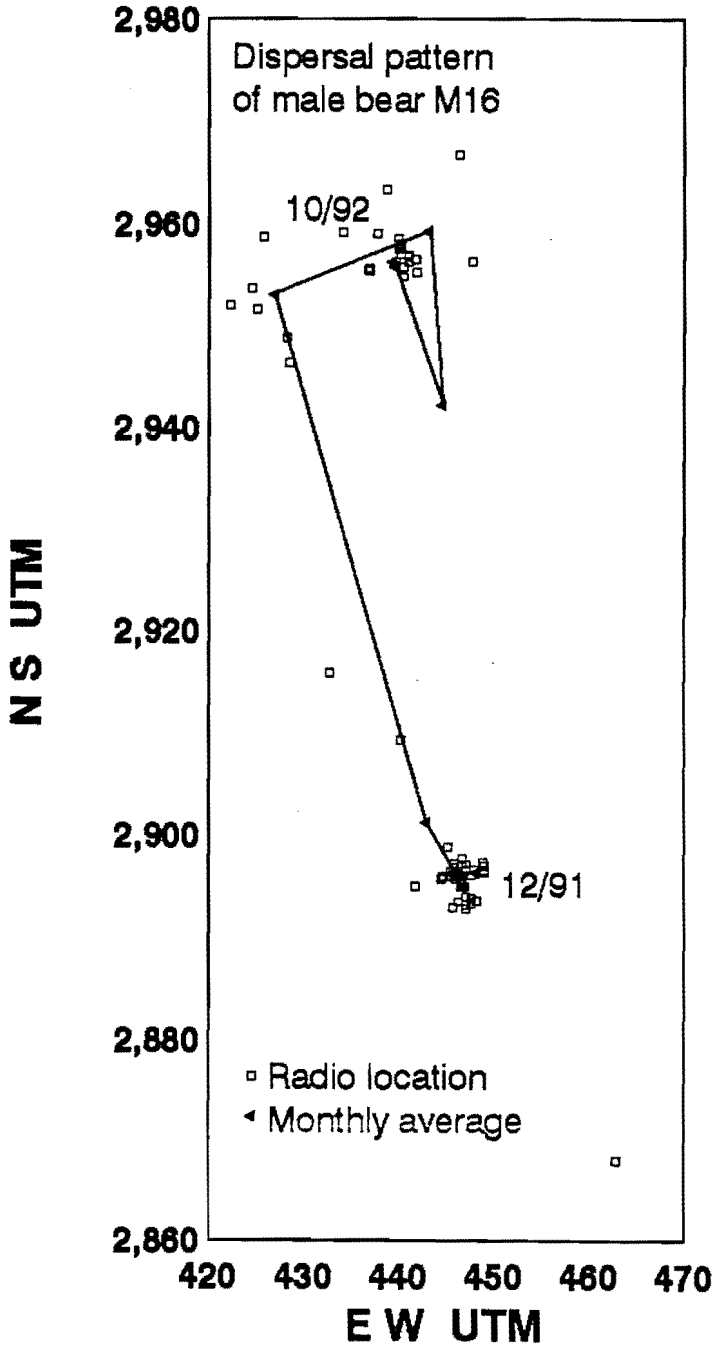


Figure 6.23. Dispersal movements of subadult male black bear M16, 1991-1992.

Table 6.9. Causes of death of black bears in south Florida, 1986-1994.

Black bear ID#	Age at death	Cause of death
F06	2.9	Hit by car
M01	2.5	Destroyed as nuisance
M03	Adult	Hit by car
M04	2.8	Poached
M09	3.5	Poached
M10	2.5	Intraspecific aggression
M11	2.5	Poached
M12	15.0	Poached
M18	12.0	Unknown
M31	14.0	Poached
M32	2.5	Hit by car

Table 6.10. Earliest documented age of first reproduction among female black bears and cougars in North America.

Location	Age	Reference
	Black bears	
Florida	2.5	This study
Pennsylvania	2.5	Alt 1989
Virginia	2.5	Raybourne 1976
North Carolina	2.5	Collins 1973
New York	2.5	Sauer 1975
Vermont	2.5	Willey 1980
Tennessee	3.5	McLean 1991
Great Dismal Swamp	3.5	Hellgren & Vaughan 1988
Michigan	3.5	Erickson et al. 1964
Minnesota	3.5	Rogers 1976
Massachusetts	3.5	Elowe & Dodge 1989
Washington	3.5	Lindzey & Meslow 1977
Colorado	3.5	Beck 1991
Alaska	4.5	Schwartz & Franzmann 1991
Idaho	4.5	Reynolds & Beecham 1980
Alberta	5.5	Ruff 1978
Montana	5.5	Jonkel & Cowan 1971
	Cougars	
Florida	1.5	This study
New Mexico	1.3	Logan et al. 1990
Nevada	1.8	Ashman et al. 1983
Alberta	2.4	Alberta Forestry, Lands & Wildlife 1992
Wyoming	3.0	Logan et al. 1986
Idaho	4.0	Seidensticker et al. 1973

M01, despite his relatively young age (2.5 years), was observed before his death with an uncollared adult female black bear in Highlands County during the breeding season. Among five subadult female black bears, three (F06, F14, and F15) gave birth to litters on their third birthdays without observed long-distance dispersals. These observations suggest that first reproduction in both black bear sexes occurs before three years of age. Although most black bears dispersed <50 km (Figs. 6.23-6.33), long dispersal events may be prerequisites to early breeding in males, whereas female bears are similar to female panthers in that they are usually recruited readily into the population without long dispersal. A comparison with other populations (Table 6.10) suggests that latitude does not influence age at first reproduction in female black bears. More likely, local nutrition explains the observed regional differences (see Appendix B). Apparently, abundant, high-energy mast supplies in locales such as Pennsylvania (Alt 1980) encourage early maturation in some temperate climates, whereas a long growing season and a high diversity of nutritious foods in south Florida results in comparable growth and demographic patterns.

Among 12 subadult male black bear dispersal events, only one (M10) was ended by intraspecific aggression (Table 6.9). While it is possible that transmitter failures and break-away collar drops may have preceded the conclusion of other dispersal events, this was the only group that demonstrated the ability to successfully negotiate human-made barriers such as the Caloosahatchee River and emigrate from south Florida (Figs. 6.22 and 6.23). As adults, all three species utilized anthropogenic habitats, but only black bears have a well-documented history in Florida as habitual nuisances. Black bears throughout Florida prey on honey bees (Apis mellifera) (Maehr and Brady 1982, Maehr 1984) and

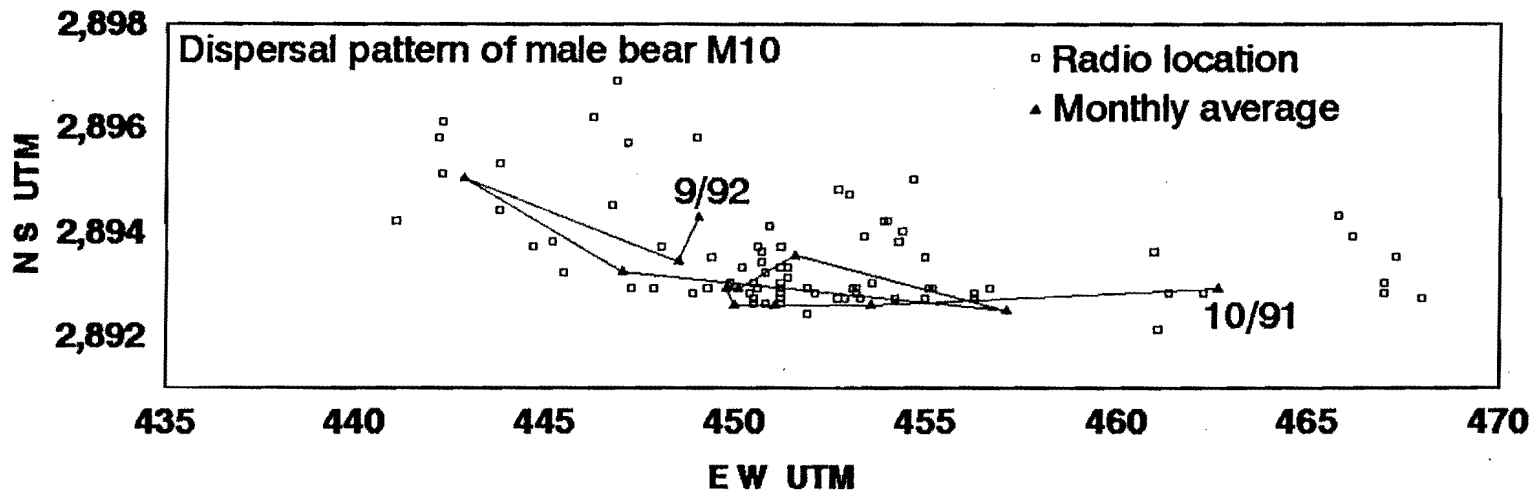


Figure 6.24. Dispersal movements of subadult male black bear M10, 1991-1992.

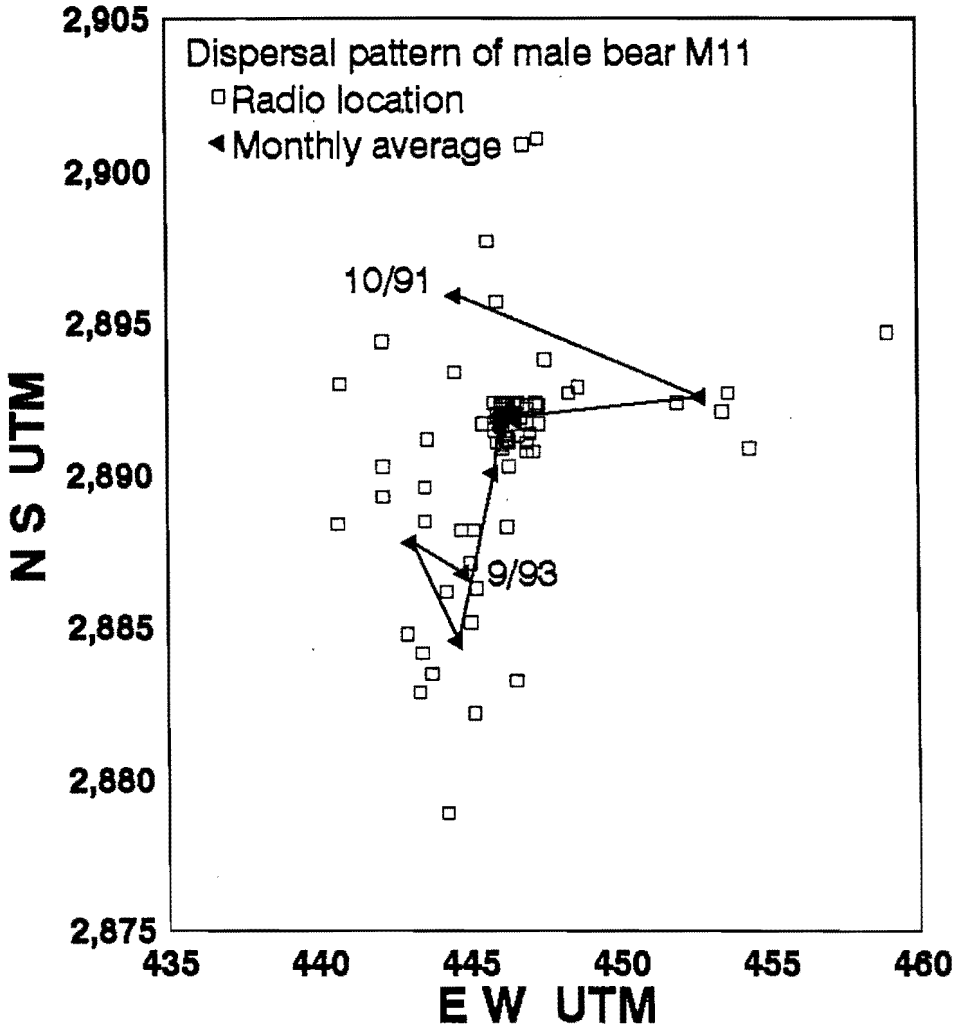


Figure 6.25. Dispersal movements of subadult male black bear M11, 1991-1993.

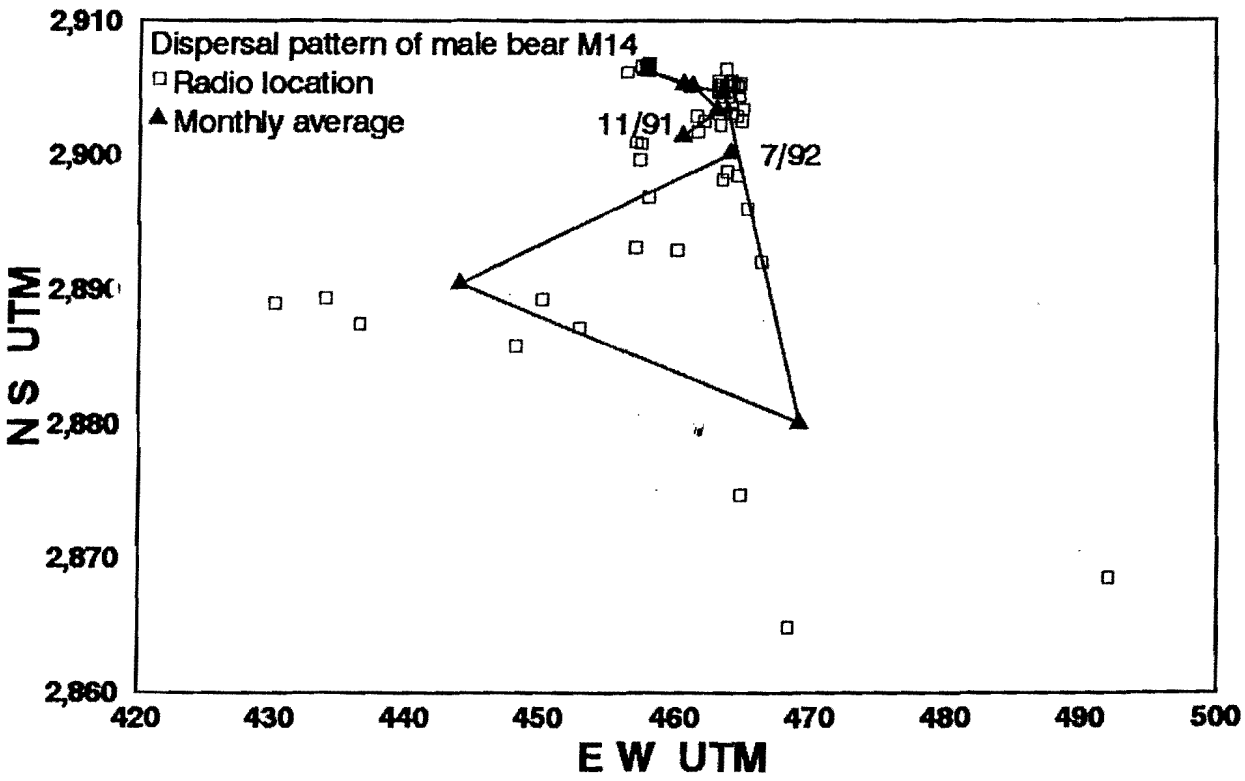


Figure 6.26. Dispersal movements of subadult male black bear M14, 1991-1992.

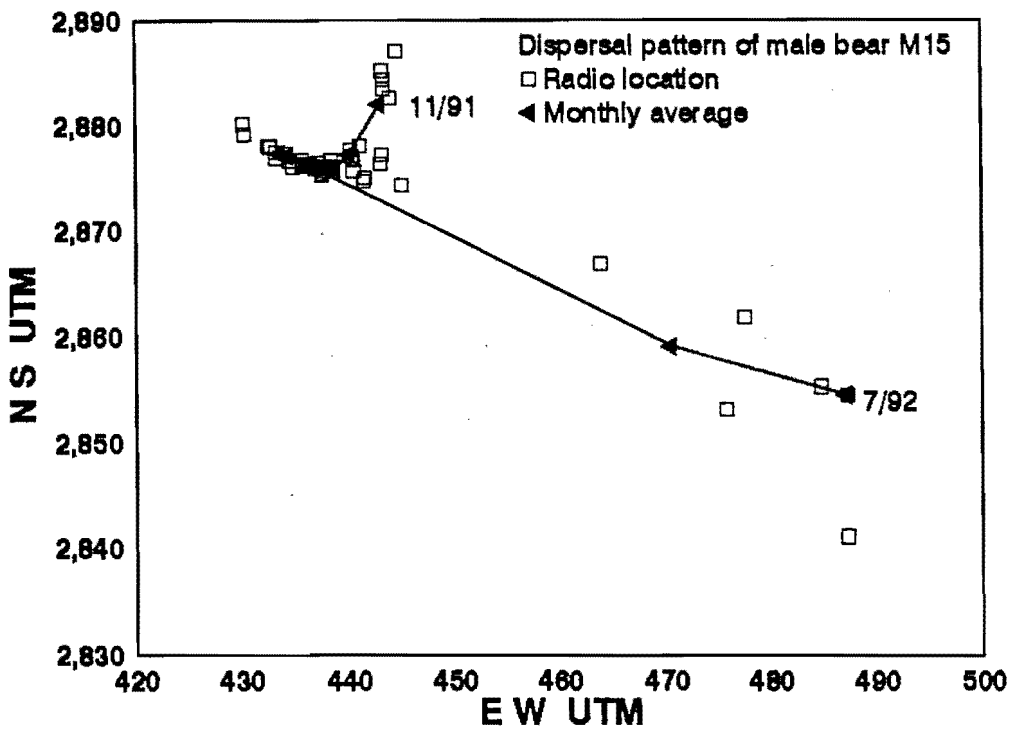


Figure 6.27. Dispersal movements of subadult male black bear M15, 1991-1992.

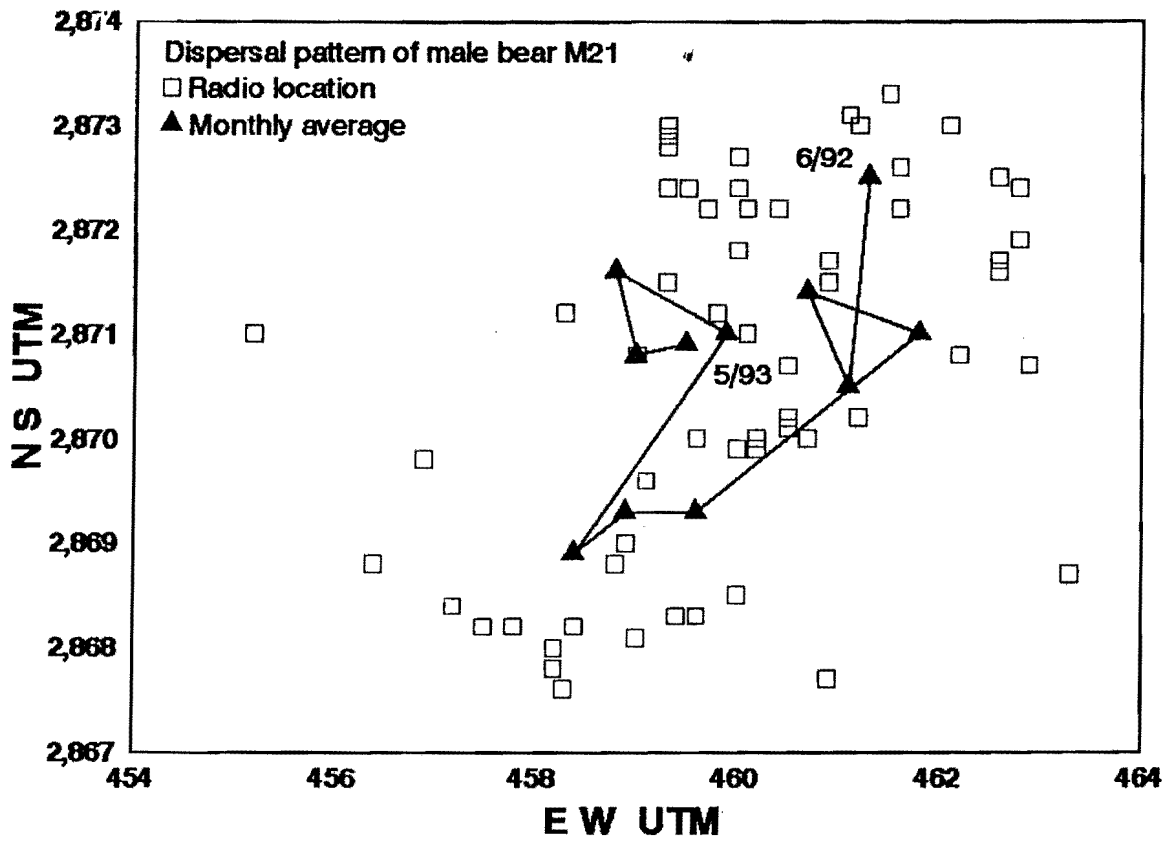


Figure 6.28. Dispersal movements of subadult male black bear M21, 1992-1993.

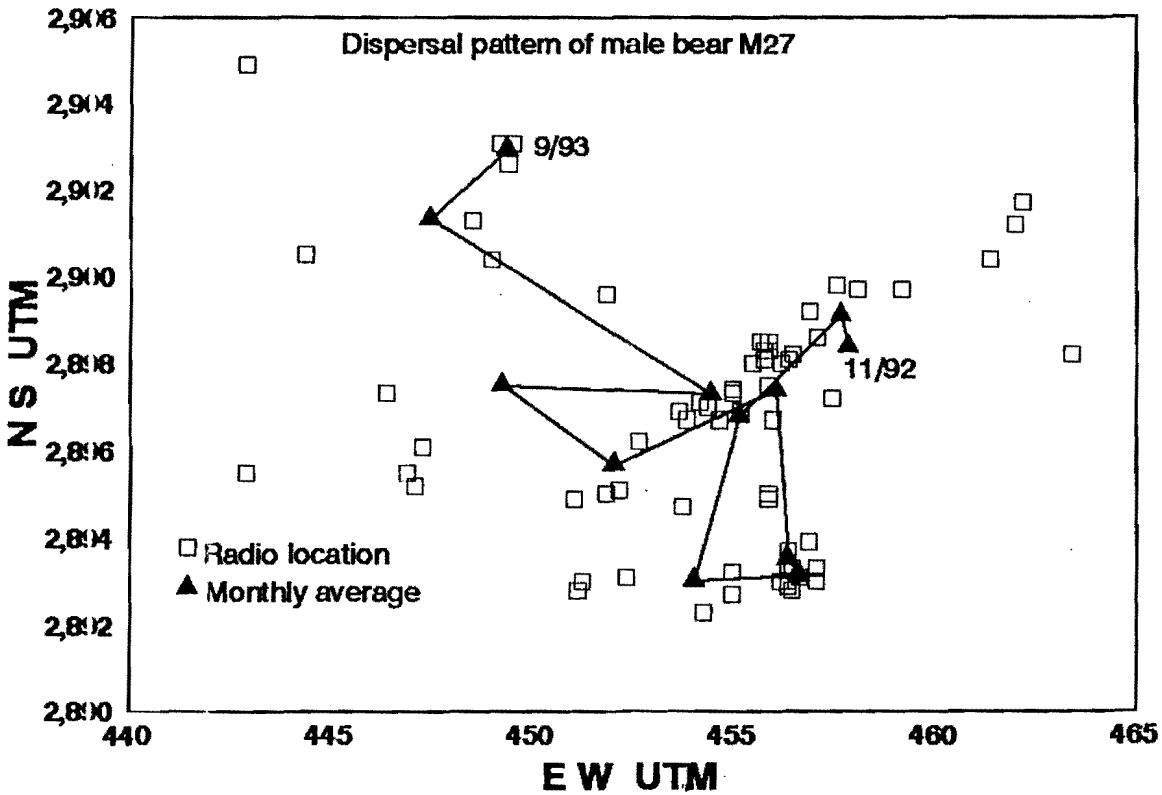


Figure 6.29. Dispersal movements of subadult male black bear M27, 1992-1993.

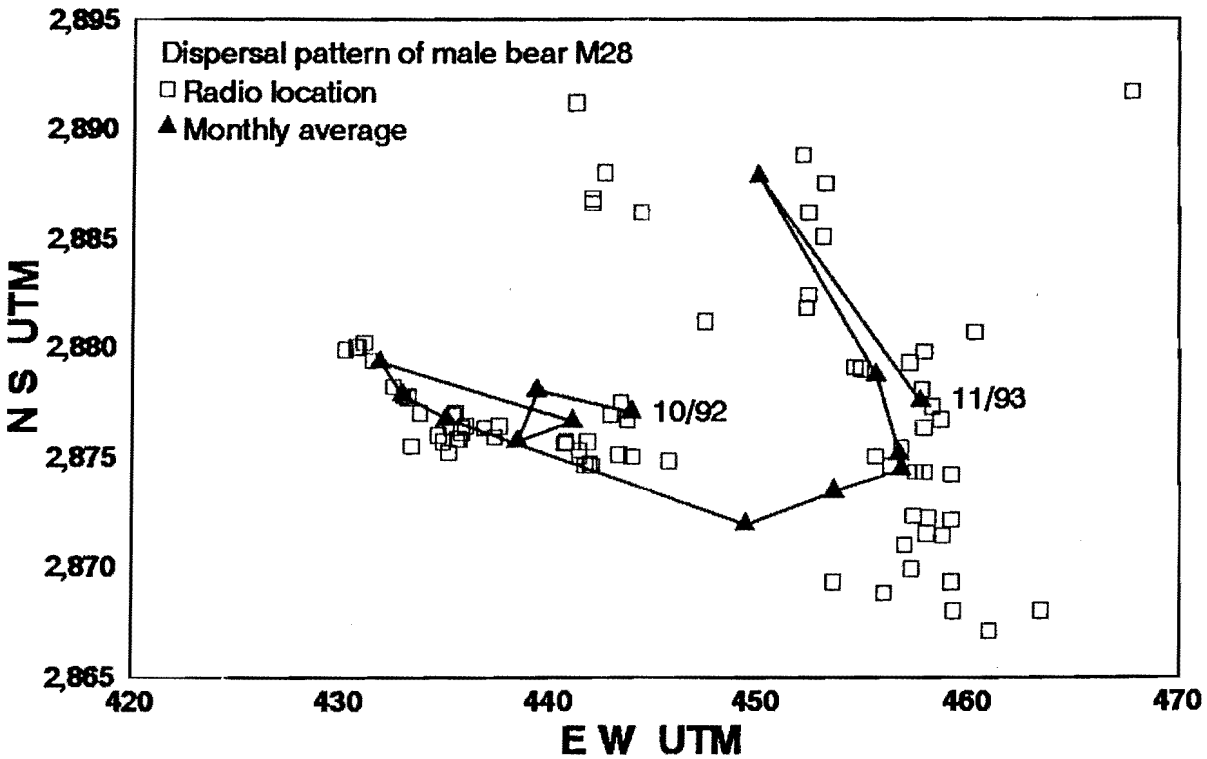


Figure 6.30. Dispersal movements of subadult male black bear M28, 1992-1993.

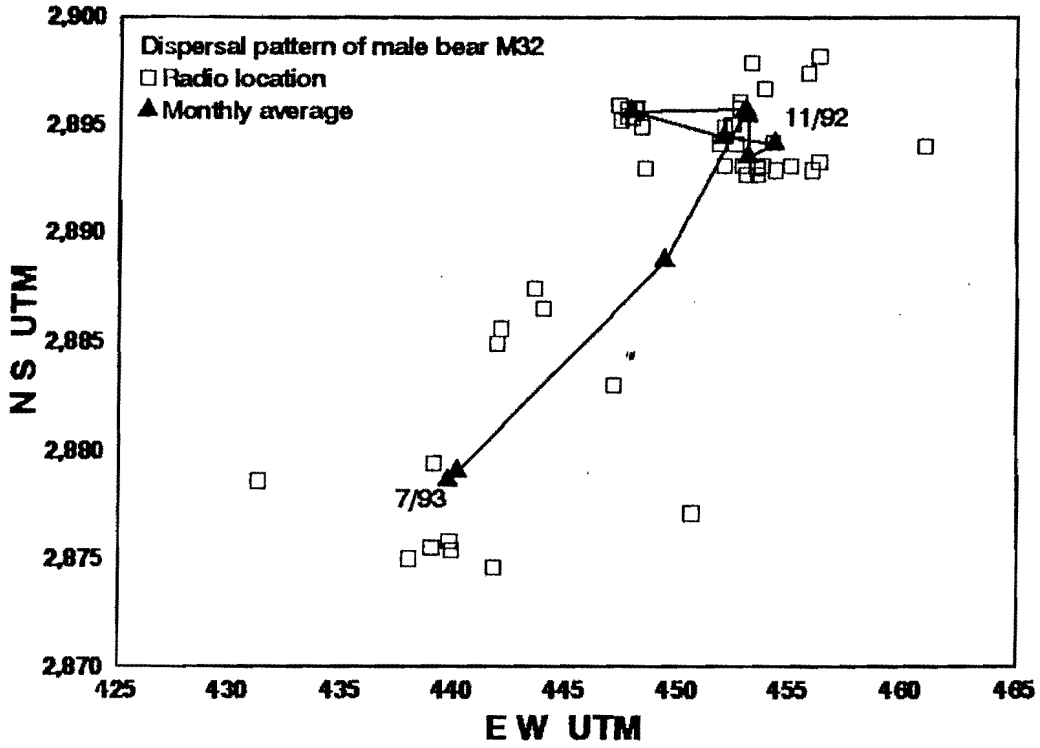


Figure 6.31. Dispersal movements of subadult male black bear M32, 1992-1993.

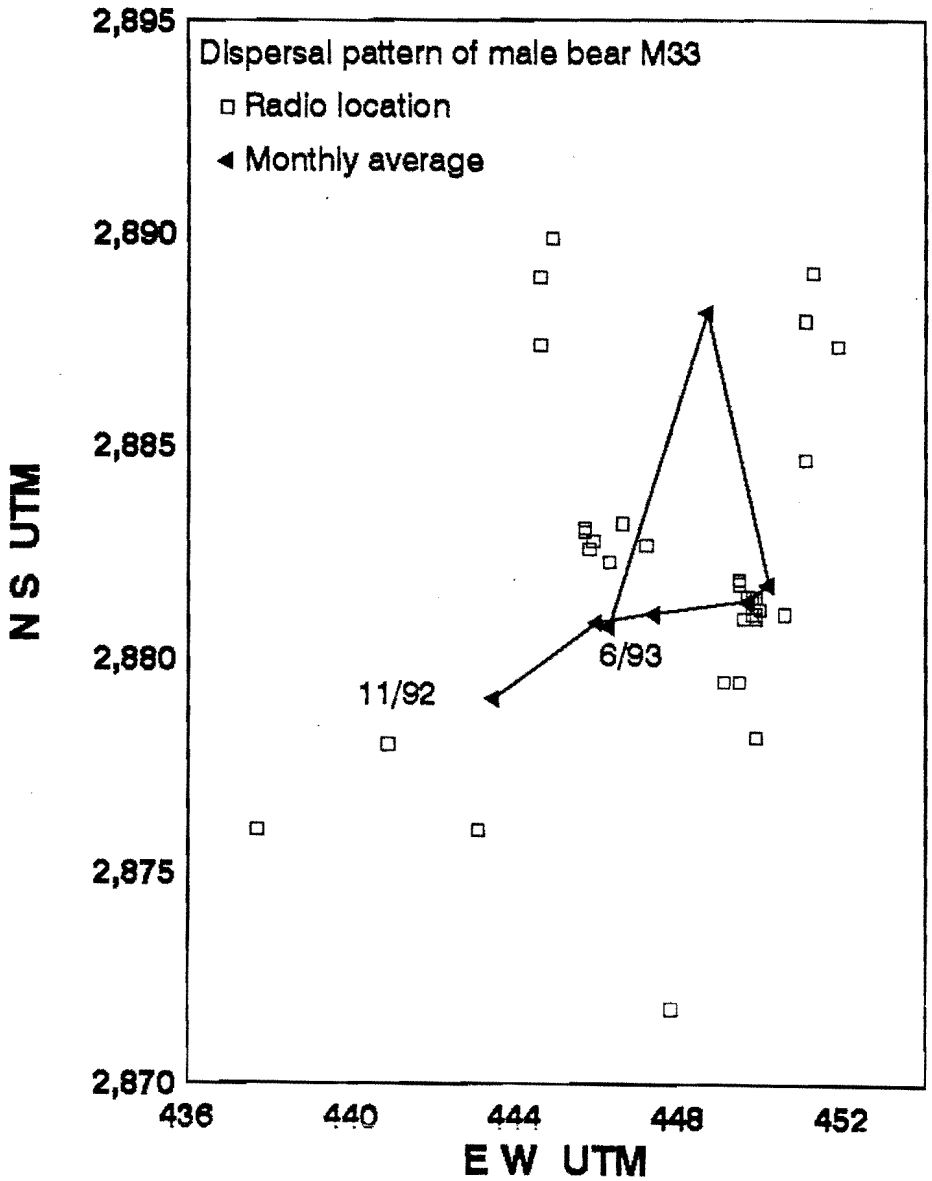


Figure 6.32. Dispersal movements of subadult male black bear M33, 1992-1993.

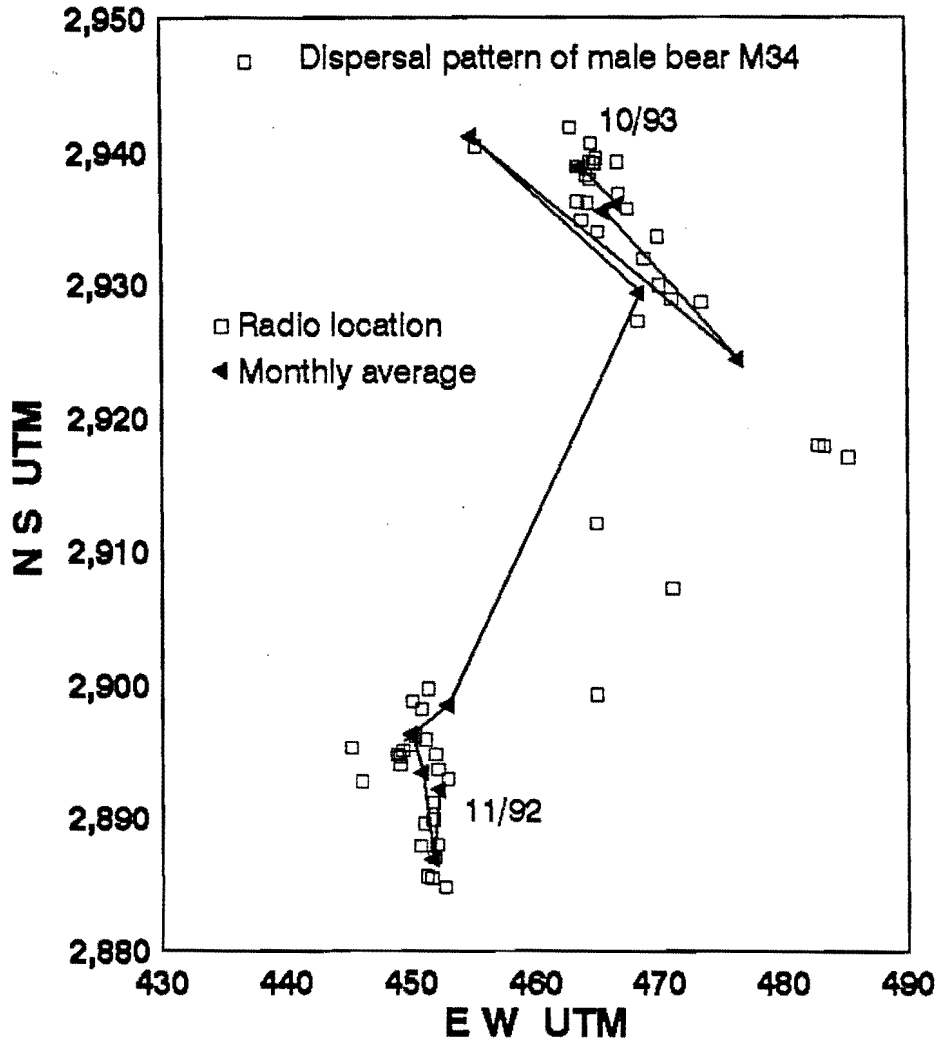


Figure 6.33. Dispersal movements of subadult male black bear M34, 1992-1993.

during this study, bears are also known to have eaten domestic hogs, domestic rabbits, chickens, household garbage, and feed intended for domestic livestock and wild birds. Most of these conflicts with people and their property likely involved dispersal-aged males as evidenced by the high proportion of 2.5-3.5 year-olds that were illegally killed by people.

Both bobcat and panther have been known to take domestic livestock in Florida (Maehr and Brady 1986, Maehr et al. 1990), but not with the frequency that bears have. While human developments in south Florida have eliminated habitat for native wildlife, obligate carnivores suffer more directly from these landscape changes because these alterations also tend to reduce or eliminate prey species. It is true that black bears suffer direct mortality from intolerant humans in this urban/wilderness interface, but the population is enhanced overall by the availability of surplus habitat for dispersing males and occasional reproduction by females in these peripheral areas. Many black bear foods such as saw palmetto, cabbage palm, and oaks are abundant in areas where human residences exceed 25 per km^2 such as in the northern Golden Gate Estates in western Collier County. It may be the same tolerance and opportunism that allows use of low-density suburban areas that encourages some black bears to abandon areas of continuous forest and disperse across open expanses. As a result, black bears are capable of maintaining demographic linkages with populations separated by at least 50 km of non-breeding range. Panthers and bobcats in south Florida, on the other hand, appear to be isolated from other populations in the state.

Black bears and panthers in south Florida exhibit varying degrees of natal philopatry (Waser and Jones 1983). For both species, males were most likely to travel long distances and exceeded the typical distances moved by adults. All male panthers appeared to make deliberate attempts to leave their natal ranges, but were seldom successful. Male black bears on the other hand demonstrated a dichotomy of dispersal strategies. Four of 12 male black bears dispersed >45 km from natal areas in primarily straight-line directions. The eight other male bears dispersed <25 km with mostly circuitous movements. Although male panther dispersal appears to be universal regardless of the availability of adult home range vacancies (Seidensticker et al. 1973, Hemker 1984, Laing and Lindzey 1993), the consistency with which male panthers left their natal ranges suggests that "habitat saturation" (Waser and Jones 1983) may drive these dispersal events. At no time during the study was a vacant resident male home range available to a subadult male panther from the same territory. The variability in dispersal patterns of male black bears suggests that habitat saturation as well as "advantages of familiarity with the natal range" (Waser and Jones 1983) are operative. It is also possible that faster turnover in resident adult male black bears created more frequent opportunities for some subadult males or that food resources and intraspecific tolerance were sufficient to reduce the need to disperse.

Habitat saturation was not as apparent among female panthers which dispersed short distances from natal ranges and in one case reproduced in her natal range. Familiarity with the natal range may be a compelling factor encouraging philopatry among female panthers inasmuch as adequate prey are necessary for successful reproduction.

Abundant prey may help to explain the social tolerance and early age of first reproduction exhibited by female panthers. Similar forces likely influence female black bears, but at least one (F16) exhibited a long dispersal event that may have been related to locally high female density. Spatial patchiness of resources may be more important to female black bears, however, than to any other species/gender group examined in this study. While males may enhance reproductive fitness when seeking out widely distributed food supplies, females can afford to move widely only when pregnant or without cubs. Successful reproduction likely depends on the ability of a relatively small area to provide adult females with ample food and denning resources which can be unevenly distributed. The relatively early age of first reproduction in female panthers and black bears is evidence that portions of the south Florida landscape compare favorably with those of other populations of these species (Table 6.10).

All three species in this study are capable of extensive dispersal movements. Although subadult bobcats were not well-represented in this analysis, maximum bobcat dispersal distances have been reported as 37 km (Robinson and Grand 1958), 75.2 km (Hamilton 1982), 136 km (Berg 1979), 158 (Bailey 1974), and 182 km (Knick and Bailey 1986). Average dispersal distances in these studies ranged from 33.4 to 37 km (Anderson 1987). Fewer studies describe dispersal characteristics of cougars and black bears. Pelton (1982) presumed that subadult black bears moved more widely than adults and Rogers (1987a) confirmed this for a population in Minnesota. Early cougar studies documented a handful of dispersal events (Seidensticker et al. 1973, Ashman et al. 1983) and more recent studies reinforced the rule that long distance dispersal is typical at least for males (Table 6.11). Although this same pattern holds true in Florida, panthers exhibit the

Table 6.11. Dispersal distances of North American cougars.

	Distance (km)		
Location	**Males**	**Females**	**Reference**
Florida	7-43	9-14	This study
Alberta	150	55	Alberta Forestry, Lands, and Wildlife 1992
Colorado	23-151	17-54	Anderson et al. 1992
Idaho	40-88	48	Seidensticker et al. 1973
Nevada	57	36	Ashman et al. 1983
New Mexico	104	51	Sweanor 1990
Utah	118-120	35	Hemker et al. 1984
Wyoming	274	-	Logan et al. 1986

shortest dispersal distances among all North American cougar populations. Of importance to demographic stability is the observation that a surplus of non-resident animals is necessary for the rapid replacement of lost residents (Maehr et al. 1991a, Laing and Lindzey 1993). In western states female recruitment occurred only after the deaths of same-gender residents (Seidensticker et al. 1973, Hemker et al. 1984). While this appeared to be the case for male Florida panthers, females were readily recruited into the population as soon as they were capable of reproduction. This suggests that adult male home ranges are saturated in south Florida, that vacancies exist among female home ranges, or that female social characteristics are more flexible than those of males.

When compared to western cougars, Florida panthers demonstrated reduced effective dispersal capability. Although some male panthers moved widely following independence from their mothers, the end of most dispersal events resulted in retracing movements that took these animals closer to their natal ranges. All three subadult females established satellite home ranges that were adjacent to or overlapping with their mothers' home ranges. Given the more continuous nature of forested and rugged terrain in western cougar range, it appears that limited habitat is the single most important factor behind demographic differences between Florida panthers and their western conspecifics. Although they have been the subject of more study in North America than cougars, less is known about black bear dispersal patterns. Rogers (1987a) and Elowe (1987), however, documented male dispersal events that exceeded 200 km. On average, black bears in south Florida did not approach this distance, but the movements of M01 suggest that black bears have not experienced the same dispersal restrictions as have panthers. Rogers

(1987a) found that females dispersed short distances and often established home ranges within or adjacent to their natal ranges. Thus, black bears in south Florida maintain dispersal patterns that are similar to those of their North American conspecifics.

Swingland (1983) suggested that populations in stable tropical environments tended to exhibit intraspecific variability in dispersal distance. Within genders, panthers demonstrated consistent dispersal patterns whereas black bears were relatively variable. Clearly, local environmental conditions do not explain these interspecific differences inasmuch as black bears and panthers occupy the same space. Further, because black bear dispersal patterns in south Florida are very similar to those reported for black bears in Minnesota (Rogers 1987b), climate appears to have little influence on this aspect of black bear ecology. It is likely that subadult panthers and black bears differ in the way they disperse because of different natural history constraints. Despite similar reproductive output and reproductive interval (two young every two years), adult panthers differ from adult black bears by being more rigid in maintaining exclusive home ranges, less tolerant of same sex conspecifics, and much more regular in their use of home ranges. It may be the variability in the part of the environment that black bears are most dependent on that sets the stage for variation in dispersal. Individual black bears can benefit from the knowledge of and the ability to travel to widely scattered food supplies, and a temporary abandonment of a home range during fall does not reduce an individual's reproductive fitness because of a distinct summer breeding season. Other bears may benefit from maintaining permanent occupancy in a smaller area that meets their nutritional and reproductive requirements. Because universal traits of occupied panther range appear to

be an evenly but widely distributed food supply and year-round breeding, a single strategy for colonizing vacant range or for replacing lost residents is sufficient for maintaining demographic and genetic stability.

Current efforts to manage Florida panthers are based on the presumption that limited immigration into the south Florida population has necessitated the creation of artificial linkages with individuals from a disjunct population (Maehr and Caddick 1995). Subspecific hybridization in the wild is now underway despite normal demographics (Appendix C), the equivocal nature of panther distribution in the state (Appendix D), and despite the potential consequences of outbreeding in this small population (Maehr and Caddick 1995). Because dispersal success in carnivores is directly related to turnover of residents, total population size is an important influence on the rate of interchange of individuals within the population. Larger populations should be more capable of absorbing dispersing individuals and encouraging maintenance of healthy demographics and genetic variability. Habitat patch size has frequently been related to population extinction probabilities (Jones and Diamond 1976, Merriam 1995) and dispersal between patches becomes more important with smaller patch size. Although all three native carnivores inhabit a roughly comparable area, their respective population sizes are differentially influenced by spatial requirements, individual tolerance of conspecifics, and diet. Thus, large home range size, relatively low spatial overlap among individuals, and widely dispersed food, limit the south Florida panther population to 70-80 individuals (Maehr et al. 1991a).

The minimum population size of bobcats in south Florida is at least 2290 based on the density estimate of Wassmer et al. (1988), and a minimum occupiable area of 8810 km^2 (Maehr 1990). Using the minimum adult population of bears in the Florida Panther National Wildlife Refuge (14/121 km^2) and extrapolating this minimum density over occupied panther range, the minimum population size of black bears in south Florida is 1020. These numbers are likely conservative because bobcats and black bears use several habitat types that panthers avoid, and field sign indicated that there were many bears that avoided trapping. Populations of these sizes should be capable of maintaining adequate levels of genetic diversity over many generations without recruitment from disjunct populations (Meffe and Carroll 1994:158), assuming that sea level rise or unforeseen events do not cause population collapses.

Clearly, immigration into the south Florida panther population is an important consideration for long-term management. However, the rates of managed introgression should be sensitive to the demographics of the target population. Given that for every 10 breeding adult female panthers, two will die in a 10 year period (based on observed mortality in southwest Florida from 1986-1994), a reasonable rate of infusion from outside of the known south Florida population would be one adult female every five years. Higher rates have the potential to promote genetic swamping. A relatively high population density of bobcats suggests that demographic and genetic stability can be maintained in an isolated south Florida landscape. Although black bears exist at lower densities than bobcats, demographic linkages with disjunct populations will ameliorate the effects of reduced population size as long as conditions conducive to crossing the Caloosahatchee

River are maintained and the population in Highlands County persists. Unfortunately, factors that encourage or prevent crossings are unknown, the status of the Highlands County black bear population is questionable, and this area failed to be considered a strategic habitat conservation area by the state of Florida (Cox et al. 1994).

CHAPTER 7

SYNTHESIS AND CONCLUSIONS

Errington (1957a, 1957b) repeatedly warned against oversimplifying the ecology of species with generalizations. His observation that dispersing muskrats (Ondatra zibethica) "may travel far or they may not" (Errington 1957a:9) reflected the variation inherent in populations when viewed from the perspective of the individual. The same caveats can be applied to any aspect of panther, black bear, and bobcat ecology in south Florida, but the generalizations presented in the preceding chapters illustrate important contrasts that would otherwise be lost amid a confusion of individuals. There is no doubt that the close monitoring of individuals also revealed differences among species that are important to their conservation. Not all black bears dispersed widely, but some of both sexes did so, and two of them negotiated a landscape feature that has contained all known panther dispersal for a decade. Although few bobcats were monitored in this study, the dispersal movements of two females exceeded those of the three female panthers that were captured as kittens and tracked through adulthood.

All three species are closely linked to forested habitats, but differences in their use of the south Florida landscape were evident. Black bears and bobcats were more tolerant of anthropogenic influences, and bears chose den sites amid less forest cover than did

panthers. Even though roads had less of a negative influence on black bears than panthers in terms of den site selection, some bears chose den sites such as hollow stumps that were more covert than any panther den discovered to date.

Even though the use of common landscape features might militate against niche separation, it soon became clear that food habits significantly separated the three species more effectively than any other comparison. Thus, features such as local environmental productivity and landscape structure may be the mechanism by which similar feeding behaviors are facilitated. Scat analyses reinforced the idea that bobcats are small-prey specialists, but under the proper conditions bobcats function more like panthers by preying on white-tailed deer. Black bears utilized all of the prey species that panthers seem to prefer, but these were taken infrequently by this large omnivore.

Comparisons of home range size, habitat use, food habits, and activity patterns suggest that south Florida's native carnivores exhibit more ecological differences than similarities. Bobcats, black bears, and Florida panthers experience seasonally variable habitat-use overlap ranging from moderate to high, and home ranges can overlap entirely. But contrasting activity patterns and minimal diet overlap suggest that the potential for competition between any two of these species is low. Perhaps the most influential factors driving the observed differences have little to do with the size of the organisms and the foods on which they depend, but have more to do with the scales at which they seek their prey. Bobcats depend on small vertebrates that exhibit unchanging and/or temporally predictable availability within static home ranges. Panthers depend on large prey that are widely scattered and reproduce slowly compared to bobcat prey, thus efficient panther

predation must be distributed widely, but more evenly in space and time. Panthers are similar to bobcats in utilizing the same area regardless of season. Black bears exhibit small movements around concentrated food supplies and apparently focus on seed sources even at the level of the individual plant (i.e. live oak, cabbage palm). Plant phenology seems to cause the home range shifts that change bear distribution seasonally. Further, some bears restrict their activities to only a few square meters for up to four months while denning.

South Florida's native sympatric carnivores not only sample and react to the landscape at different scales, they also respond to it with different seasonal patterns. Panthers show nearly no seasonal variation in their use of food and space (Fig. 7.1). Their only possible seasonal response is an increase in mating activity during cooler months, but breeding can occur year-round. Black bears represent the opposite extreme in seasonal responses inasmuch as dietary, spatial, and reproductive ecologies are more closely linked to nutritional and abiotic factors. Bobcats exhibit no seasonal variation in home range use, and only moderate cyclicity in diet (e.g. eating neotropical and over-wintering migrants), and possibly reproduction.

It is of interest that the species with the smallest spatial requirements may have the farthest-reaching impacts on other organisms, inasmuch as bobcats prey on birds that may breed greater than 1000 km away (Fig. 7.1). Black bears function as seed disseminators, an activity that enhances reproductive fitness in many plant species, but also encourages the spread of favored food species such as the noxious exotic Brazilian pepper. Panthers exert a continuous pressure on white-tailed deer, and thus, maintain an evolutionary relationship that exists nowhere else in eastern North America.

ECOLOGICAL VARIATION AMONG SOUTH FLORIDA CARNIVORES

SEASONALITY OF:	BOBCATS	BEARS	PANTHERS
DIET	Moderate	High	None
SPACE &	None	High	None
REPRODUCTION	Moderate	High	Slight
PROCESSES & PHENOMENA AFFECTING ECOLOGY AND DISTRIBUTION	Over-wintering birds Spring fawning	Plant phenology Abiotic cues Denning	Forest systems Mate distribution
INFLUENCE ON THE LANDSCAPE	Migrant bird demographics	Seed dissemination/ succession	Prey fitness & behavior

Figure 7.1. Comparison of major ecological variables influencing south Florida large carnivore distribution and demographics.

Anthropogenic changes to the south Florida landscape have created an environment that is very different from pre-Columbian conditions, but prehistoric humans such as the Calusa were already an important predator of white-tailed deer (Wing 1965) and most likely competed directly with panthers, bobcats, and black bears for this and other foods such as birds and mast. Although there is no direct evidence that aboriginal Americans did not harvest large carnivores directly for food, clothing, and ceremony, this possible interference competition does not appear to have limited the distribution of Florida's native carnivores. Indeed, the discovery in 1895 of an ancient wooden half human-half panther sculpture in southern Collier County (Tinsley 1987) suggests that local primitive cultures at least revered one of these species. Clearly, Florida's remaining native carnivores have already demonstrated their ability to tolerate human intrusions, but the intensity of prehistoric interactions between them were of very different nature than they experience from humans today. Nonetheless, panthers, black bears, and bobcats all have managed to maintain typical patterns of dispersion and demographics throughout a large portion of south Florida.

Peninsula effects and fluctuating coastlines may have added long-term instability to Florida's environment that may have overshadowed any influences that Amerindians had, and that may have naturally reduced its carnivore carrying capacity. Thus, tropical species such as jaguarundis (Felis yagouaroundi), ocelots (F. pardalis), and jaguars (Panthera onca), which tend to exist at low densities in the northern tropics (Eisenberg 1989), and which probably occurred in Florida during the Holocene, were selected against as humans altered a landscape that already was marginally suitable for supporting such a diverse

carnivore community. This same landscape was severed from equatorial land masses as recently as 4,000 years ago by sea level rise, thus an important source for tropical terrestrial colonizers was lost. Moreover, the structure of Florida's forests is far less complex than that of the tropics where multiple canopies and a varied ground cover (Richards 1952) provide as many as nine felid niches (Sunquist 1987). Further, because south Florida approaches the geography of an island, one would expect even fewer species as the result of competitive exclusion or elimination than a continental land mass of comparable size (McArthur 1972). The end result of a peninsula effect, millennia of human interference competition, isolation from recolonization sources, and the more simple forest structure in Florida is the collection of solitary generalist carnivores (minus the recently extirpated large canid) that persist today.

Modern panthers utilize a vertebrate-enriched prey base but are locked into an inelastic landscape envelope that stymies potential population interchange. Similarly, black bears are sustained by nutritious foods that occur at a time of year when most other seed sources are gone or are months away from ripening, and widespread drainage operations have encouraged the spread of energy-rich native food sources such as a variety of tropical palms. Bobcat diets have been augmented with the exotic rodents, black rat (Rattus rattus) and house mouse (Mus musculus), and in the urban/wilderness interface domestick stock such as chickens and rabbits. In terms of genetic interchange, south Florida is probably of sufficient size, at least in the short term, for the bobcat population to maintain "healthy" levels of genetic variability, and south Florida black bears have exhibited at least some demographic ties with bears from south-central Florida.

Perhaps the single-most important anthropogenic change relative to ecological and evolutionary processes among south Florida carnivores, was the elimination of a sympatric large canid through land-clearing and persecution. Interestingly, the danger-avoidance behavior known as treeing, a trait that is common to the three carnivores examined in this study, evolved solely for the purpose of reducing interference competition with pack-living wolves (Herrero 1978); a convergently evolved behavior that now has little natural survival value for native carnivores in south Florida. Ironically, two black bears, most of the bobcats, and every adult panther handled in this study were treed, primarily by an organized pack of wolf-like relatives (Canis familiaris). Clearly, taking advantage of this "ghost of competition past" (Connell 1980) was vital to obtaining sufficient sample sizes and in understanding the ecology of south Florida carnivores, but this instinctive behavior has not been used under natural circumstances to reduce competition for a century. The persistence of treeing, and its universal practice by south Florida's terrestrial carnivores, suggests the powerful influence that canids have had on the evolution of black bear, bobcat and panther behavior. Not only do the stereotypic treeing-escape-behaviors exhibited by south Florida carnivores suggest past interactions with wolf-like competitors, they also are strong evidence that these species are forest obligates. Interfering competitors must have been necessary for the evolution of this behavior, just as were appropriate morphology, physiology, and an abundance of trees. Although bears and panthers exhibit different denning and habitat use patterns, and they respond differently to anthropogenic influences such as roads, the presence of extensive forest cover is the common, most pervasive, and compelling link between south Florida's native carnivores.

The Return of Wild Canids to Florida

In North America, few taxa have endured more dramatic changes in abundance and distribution than the Canidae. Florida's native large canid has been absent from the state for nearly a century (Young 1946, Robson 1992). Along with extensive alterations of the native plant and prey communities, the remaining native large canids have experienced new and rapidly-changing environments due to this faunal relaxation. In pre-European times the gray wolf dominated over its canid relatives (Litvaitis 1992), and its tendency to form packs provided advantages over other, even larger carnivores. In the Hudson Bay region, Ramsay and Stirling (1984) documented gray wolves preying on polar bears. In one-on-one interactions between wolves and black bears the latter dominate. However, solitary black bears and cougars are both vulnerable to packs of wolves (Rogers and Mech 1981, White and Boyd 1989).

While wolves can dominate smaller canids (Carbyn 1982), coyotes are adaptable enough to benefit from distributional overlap with other predators. Paquet (1991, 1992) found that coyotes followed wolf packs along commonly-used trails in order to scavenge kills. Although they are also preyed upon by cougars (Boyd and O'Gara 1985), coyotes appear to dominate or benefit from all possible interactions with sympatric carnivores (Theberge and Wedeles 1989, Major and Sherburne 1987, Dekker 1983, Harrison and Bissonette 1989, Sargeant et al. 1987, Voigt and Earle 1983).

Bobcats are small prey specialists that can coexist with coyotes during times of abundant prey (Witmer and deCalesta 1986). Generally, however, where both species are present, bobcats experience reduced prey availability (Dibello et al. 1990) and potential

habitat loss (Litvaitis and Harrison 1989). Koehler and Hornocker (1991) found that cougars killed bobcats and coyotes in a three-species assemblage in Idaho. However, because coyotes often lived in groups, they suffered less interference competition from cougars than did bobcats, which are solitary.

As was noted by Hutchinson (1957:424) "The rapid spread of exotic species often gives evidence of empty niches, but such rapid spread in many instances has taken place in disturbed areas." In terms of distribution and new niche opportunities, coyotes have fared better in the last century than any other carnivore native to North America. Litvaitis (1992) suggested a dominance hierarchy whereby coyotes were subordinate to wolves but dominated red foxes; coyotes and lynx (Lynx canadensis) maintained separation because of differential adaptability to deep snow; cougars created interference for coyotes; and coyotes caused interference for bobcats. However, where coyotes colonize areas from which they were previously absent, their presence may create a burden for long-standing resident carnivores even when individual encounters may favor the coyote's competitor. Energy spent defending kills and territories, and the possible reduction in prey resources likely reduces local carrying capacity for individually dominant predators such as cougars. Little is known about coyote interactions with black bears, but because both species are omnivorous, the potential for dietary overlap exists. Coyotes prefer relatively open habitat and edges, thus the potential for competition with forest interior species such as black bears, cougars, and bobcats may increase as forests become increasingly fragmented. Further, because coyotes will also utilize forested habitats, they are a potential vector for

the spread of the noxious exotic plant, tropical soda apple (Solanum viarum) into currently uninvaded hammocks, flatwoods and other important terrestrial carnivore habitats.

Although the actual status of the coyote in Florida is still only vaguely known, the first Florida field study designed to determine coyote distribution (Appendix A) indicated that this species is now a permanent resident in south Florida. The 1995 survey revealed a distribution that extends from the southern Lake Wales Ridge to the northern Big Cypress Swamp. Coyotes prefer open terrain over heavy forest (Young and Jackson 1951, Parker 1995), but ecotones may also be important (Eisenberg 1989). Increasingly drained and/or unforested landscapes should encourage the continued migration of coyotes into south Florida where dense forests, wet summers, and larger native wolf species once excluded them. Habitat use patterns of south Florida coyotes can only be speculated upon, but the highest amount of spatial overlap with native carnivores will likely occur in habitats associated with agriculture such as improved pasture, vegetable fields, and citrus groves. Nonetheless, as coyotes increase their numbers in south Florida, drier native habitats such as pine flatwoods, scrub, dry prairie, and hardwood hammock will be used more frequently. A change in the current equilibrium among south Florida's native carnivores that might be caused by landscape changes and a non-native predator has the potential to narrow the realized niches (in the sense of Hutchinson 1957) of the natives and reduce their survival probabilities.

Dietary comparisons indicated low overlap among black bears, bobcats, and panthers. However, when a hypothetical south Florida coyote diet was constructed using data from coyote studies elsewhere (Witmer and deCalesta 1986, Litvaitis and Harrison 1989, Theberge and Wedeles 1989, and Dibello et al. 1990) and added to the food

Table 7.1. Dietary overlap among native south Florida carnivores and the coyote.

Species	Black bear	Florida panther	Bobcat	Coyote
Black bear	1	-	-	-
Florida panther	0.0155	1	-	-
Bobcat	0.0022	0.1342	1	-
Coyote	0.4259	0.3849	0.6372	1

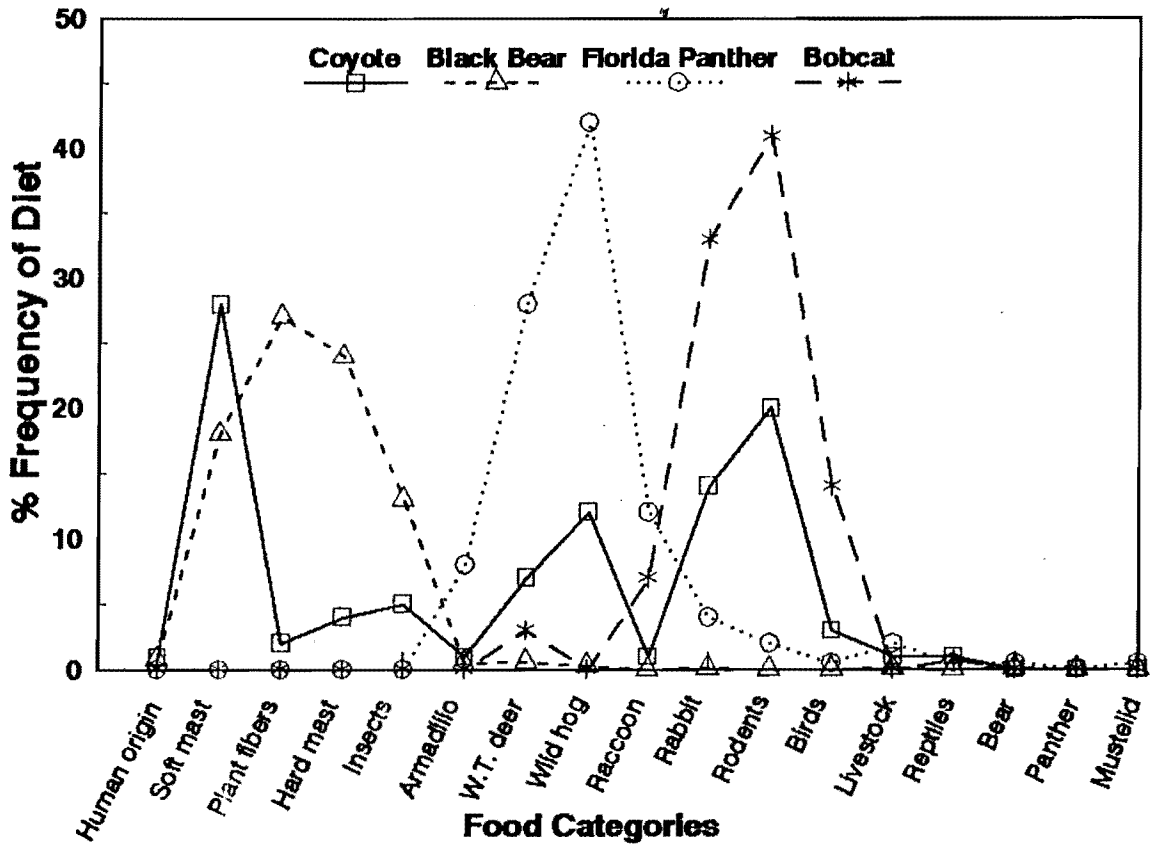


Figure 7.2. Comparison of south Florida carnivore food habits with those of a hypothetical Florida coyote diet.

resource overlap analysis, a new relation among south Florida carnivores emerged. Instead of adding a unique food resource grouping to the graph (Fig. 7.2), coyotes exhibited overlap ranging from 0.38 with panthers, 0.43 with black bears, and 0.64 with bobcats (Table 7.1). This overlap coincided with the peaks in important foods for all three native south Florida carnivores (Fig. 7.2).

Such high levels of dietary overlap, regardless of other forms of niche separation, will most likely have negative consequences on south Florida's native large carnivores. For example, white-tailed deer that are vulnerable to panther predation when feeding in forested terrain may also become vulnerable to coyotes when feeding or traveling in more open cover such as prairies and improved pasture. While it could be argued that the addition of the coyote to the fauna of south Florida is no more than a replacement for two extinct wolf species, the landscape changes that have occurred in the last 100 years have already reduced the carrying capacity for bobcats, black bears, and panthers. By virtue of these changes and their proven adaptability, coyotes will be at an advantage. Coexistence among these species has been demonstrated elsewhere, but not in an area where panther numbers are so low, and where dispersal opportunities for the widest-ranging species are so limited. Smith and Bass (1994) noted that the difference between successful reproduction and none at all in Everglades National Park appeared to hinge on the availability to female panthers of adequate numbers of white-tailed deer. In this predominantly herbaceous setting, non-reproductive females were forced to consume small or non-traditional prey such as raccoons (Procyon lotor) and alligators (Alligator mississippiensis), and eventually the population was extinguished (Bass and Maehr 1991). There is no indication that deer numbers are insufficient to support successful

Table 7.2. Comparison of home range sizes between resident adult panthers in eastern Big Cypress Swamp and resident adult panthers in northwestern Big Cypress Swamp, 1993-1994.

Northwestern Big Cypress Swamp			Eastern Big Cypress Swamp		
Panther ID#	Sex	Home range size (km^2)(n)	Panther ID#	Sex	Home range size (km^2)(n)
26	M	376.6 (147)	42	M	1881.9 (144)
40	F	195.6 (151)	23	F	402.1 (152)
48	F	157.5 (147)	38	F	530.3 (152)

panther reproduction where large tracts of dense forest occur. On the other hand, panthers in eastern Big Cypress National Preserve are probably living on a nutritional borderline. Infrequent reproduction and home range sizes that are more than 2.6 times larger for females and nearly five times larger for males than their southwest Florida counterparts (Table 7.2) (larger than any home ranges reported for the species, Anderson 1983:48), suggest that perhaps deer numbers are at the minimum density necessary to support resident panthers. Despite this, adult females from Texas have been introduced to this marginal habitat by the State of Florida in order to enhance population genetics without the removal of residents to accommodate these additional animals and increased predation on a marginal food supply. The invasion by coyotes into this part of south Florida may eliminate panthers from marginal habitat, and may reduce the carrying capacity of the only subpopulation that has exhibited demographic stability over time (Maehr and Caddick 1995). Reductions in number of breeding panthers in southwest Florida, regardless of the effects of "genetic restoration" efforts (Maehr and Caddick 1995), will likely result in a decline that cannot be compensated for.

The present high abundance of bobcats is probably the most compelling factor favoring their persistence in south Florida. Although bobcats are usually at a disadvantage when competing directly with coyotes (Litvaitis and Harrison 1989, Dibello et al. 1990), bobcats will be able to maintain adequate numbers in south Florida by utilizing smaller forest fragments than necessary to sustain panthers (Maehr and Cox 1995), and by living in more anthropogenic habitats. Further, wet and heavily forested areas such as the Fakahatchee Strand will act as refugia against encroachment by coyotes. By itself,

however, such a large forest fragment will be insufficient to ensure the long-term future of south Florida's other large carnivores.

Although black bear home ranges are smaller than those of panthers, seasonally changing habitat requirements that compel large movements make them vulnerable to changes in outlying portions of their range. For example, just as commercial collectors of saw palmetto fruit can locally decimate bear foods, resident coyotes have the potential to eliminate this popular wildlife food in areas that are 'protected' against plant harvest by humans. These new competitive influences may reduce the carrying capacity for black bears in south Florida, and thus reduce litter sizes and delay growth and maturation in females. Like bobcats, however, black bears have several habitat refuges such as the Fakahatchee Strand and the vast coastal mangrove wilderness of south Florida. Restricted nutritional opportunities caused by coyote competition may reduce overall bear numbers, but not to the point where black bear persistence will be in jeopardy. Even without saw palmetto fruit, sufficient food supplies including cabbage palm, certain insects, and Brazilian pepper will provide black bears with adequate year-round nutrition.

A Longer Range View

One approach to conservation involves the perspective of gamma, or landscape level, species. Florida panthers and black bears can be considered landscape-level species because individuals have large home ranges and utilize a variety of habitat types that may be parts of distinct and sometimes distant ecosystems (Harris 1988, Harris and Gosselink 1990). If meeting the needs of one of these species satisfies the needs of the others, then conservation dollars can be more efficiently distributed. Bobcats will certainly benefit

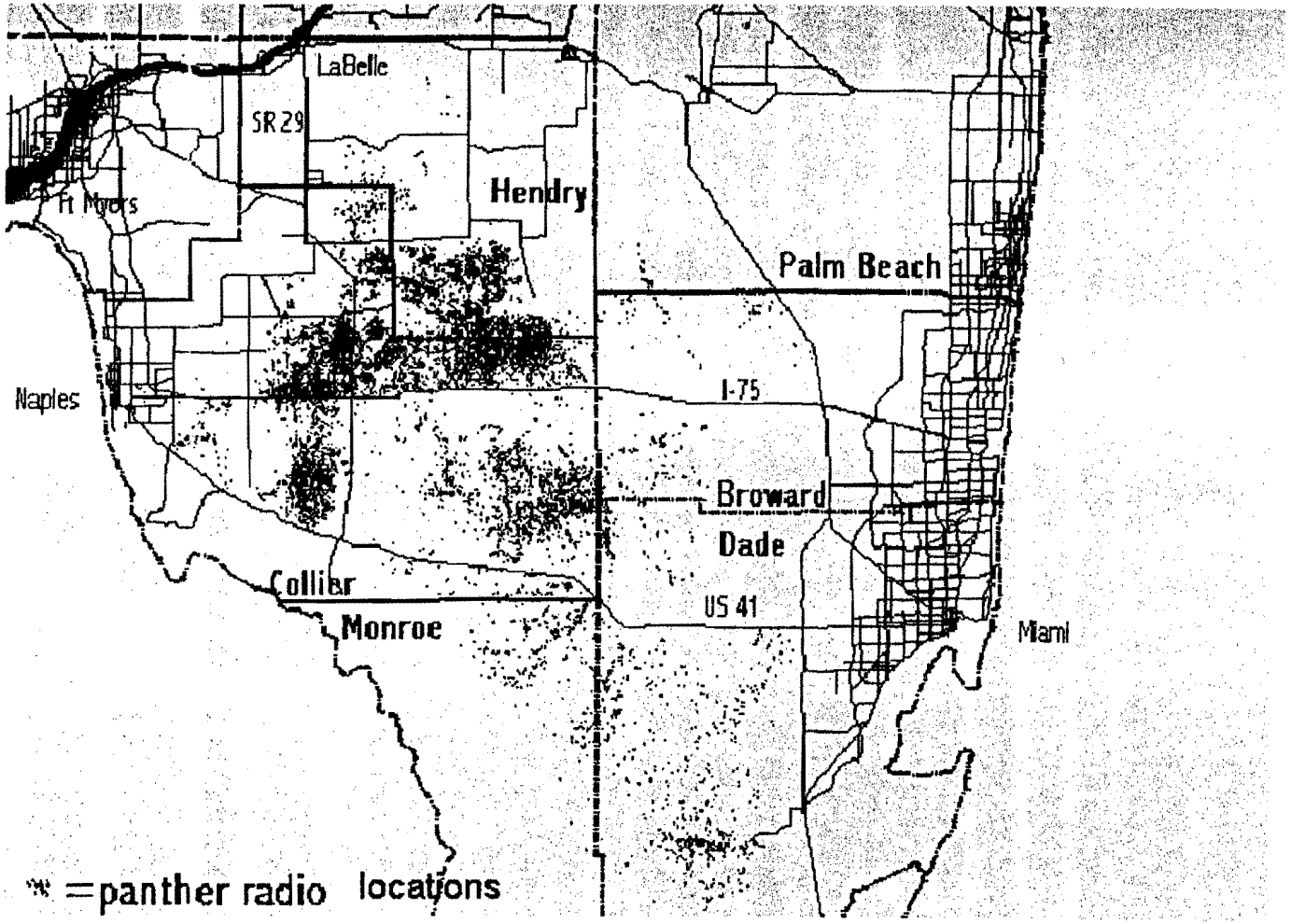


Figure 7.3. Distribution of Florida panther radio telemetry locations in south Florida, 1990 - 1995.

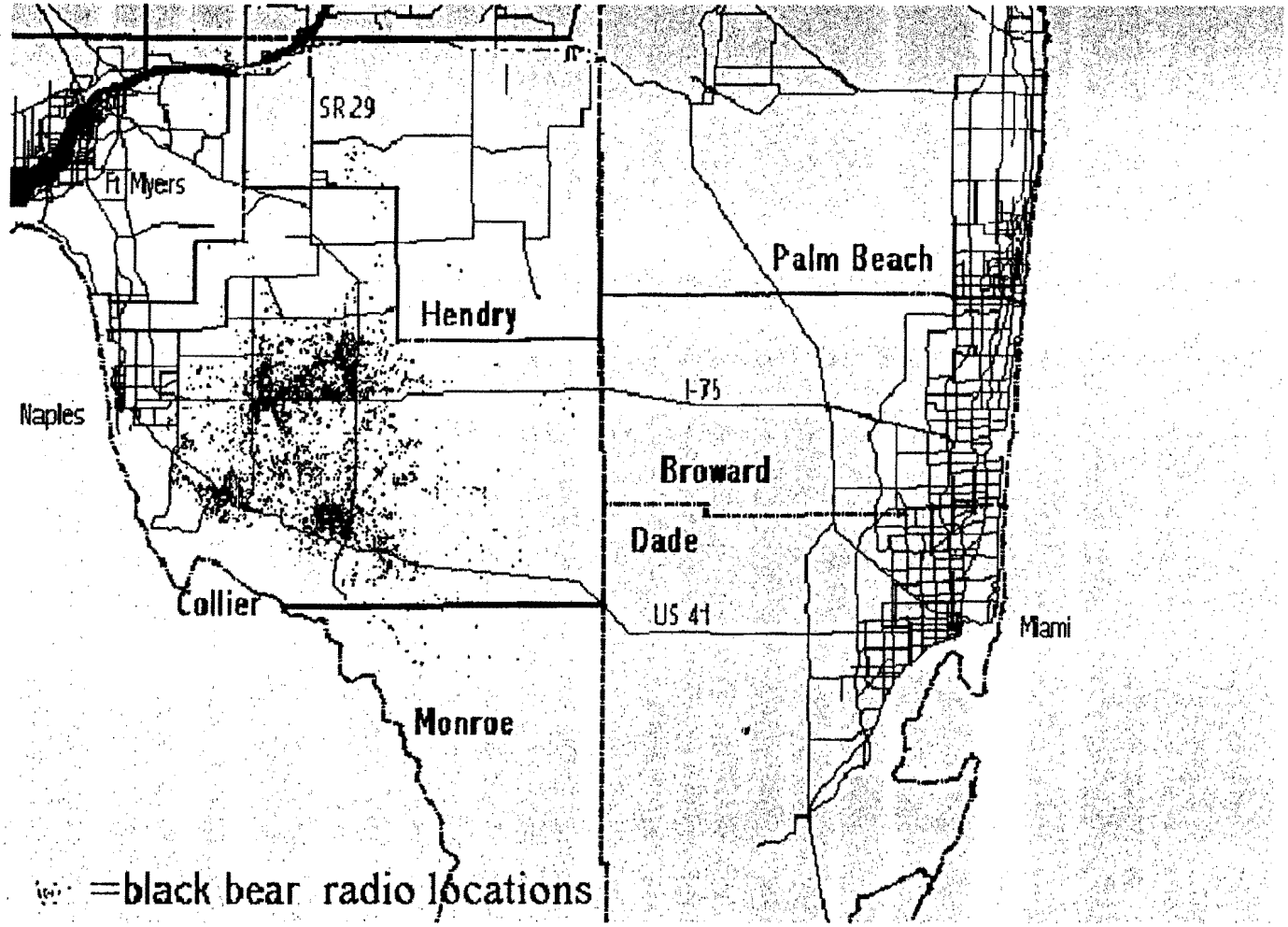


Figure 7.4. Distribution of black bear radio telemetry locations in south Florida, 1986 - 1995.

from any successful efforts to manage bears or panthers because of their relatively small space requirements, and because their range is a subset of panther and black bear distributions.

Figures 7.3 and 7.4 contrast the distribution of Florida panther (n=17,508 locations from 56 individuals, 1990 through 1995) and black bear telemetry locations (n=6,725 locations from 64 individuals, 1986 through 1995) in south Florida. Because capture efforts differed spatially and temporally between species, the distribution of telemetry points is in large part a function of field methodology. Panthers were captured throughout accessible range primarily during winter, whereas black bears were captured in less remote areas throughout the year. Further, intensive efforts were made to document reproduction in female panthers and to capture and instrument their offspring. Such efforts were not possible with the shorter-duration bear study. As a result, the map of panther locations is a better reflection of total distribution (including dispersers) than is the map for black bears. It also reflects the existence of an area previously referred to as the habitat core (Fig. 7.5). The conservation of this area, which is made up of approximately equal proportions of public and private lands, is of critical importance to the future of both species. Until now, both black bears and panthers live permanently in this area, but their apparent distributions differ outside of the core. First, panthers clearly avoid mangrove habitats as is evidenced by the lack of locations south of US 41 and west of SR 29 (Fig. 7.3). Black bears not only used these tidal forests, but established natal dens in them as well. Both panther and black bear locations become sparse the farther one travels to the southeast. Because of more consistent and wide-ranging capture efforts for panthers throughout south Florida, this is not a consequence of sampling, although such could be

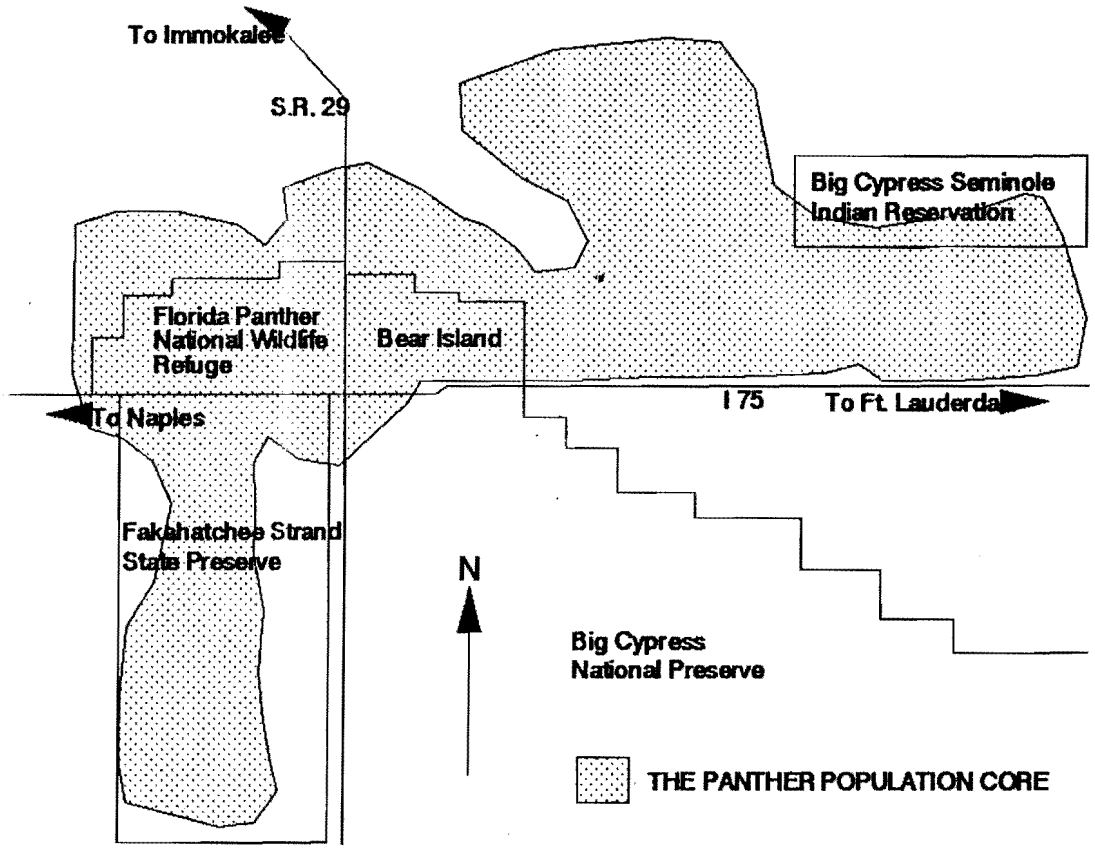


Figure 7.5. The Florida panther habitat core as suggested by the distribution of radio telemetry locations and extensive forests in south Florida.

the case for black bears. This same phenomenon may explain the lack of bear locations in southern Hendry County where panther use was concentrated. However, black bear sign was less frequently encountered during panther capture efforts than in areas such as the Fakahatchee Strand and the Big Cypress National Preserve addition lands in Collier County. It is possible that increasing forest fragmentation due to clearing for cattle ranching in southern Hendry County may be more detrimental to black bears than to panthers in this area. Black bears were also frequently found in the western Collier County suburban development, Golden Gate Estates. This suggests that where ample forest cover occurs, black bears are more tolerant of human activity and/or the loss of potential prey species such as deer and hogs, than are panthers. Thus, both species need to be considered in long-range conservation plans in south Florida. Considering the needs of only one species will leave vulnerable large portions of the range of the other.

Florida panthers are top-level carnivores that require large areas to meet their prey needs for individual maintenance and to raise young. Black bears are opportunistic carnivores that depend on widely distributed but locally concentrated plant food resources. Further, both species exert a direct influence on their plant and animal prey. For more than $2x10^6$ years an array of carnivorous Florida land mammals have tolerated fluctuating climate, sea level, and prey opportunities across an uninterrupted though constantly changing peninsula (Webb 1984, Brown 1988). Modern south Florida supports three of the five large (>10 kg) carnivores that were present before European settlement of the New World, and it is the only region in eastern North America where these three species still share a common landscape. Ironically, the two largest preserves in Florida are

probably insufficient to assure a future for this trio. The large (607,000 ha) national park and preserve complex only provides marginally suitable to inadequate habitat for panthers. Maehr and Cox (1995) concluded that the naturally occurring fragmented forests and predominantly wet herbaceous landscapes of Big Cypress National Preserve and Everglades National Park were incapable of supporting a stable panther population. Everglades National Park was home until very recently to the only subpopulation of panthers that is known to have gone extinct in the last two decades (Bass and Maehr 1991), and Big Cypress National Preserve supports fewer panthers (three adults in 1994) than preserves 5% of its size (i.e., the Florida Panther National Wildlife Refuge covers 10,120 ha and is used by as many as 10 panthers annually).

A declining gradient of panther prey abundance from northwest to southeast has been measured within panther range (McCown et al. 1991), and this may help explain the phenomenon of varying panther abundance. But an equally compelling explanation may be the landscape itself. An examination of rectangular areas of approximately 50 km^2 reveal that the pattern of forest cover from northwest to southeast also exhibits a declining trend (Fig. 7.6). Continuous forest cover such as is found in the Fakahatchee Strand and Florida Panther National Wildlife Refuge coincides with permanent panther occupation and good reproduction. Patchy forest cover such as is found in the Raccoon Point area of the Big Cypress National Preserve dominates an area that supports few Florida panthers and sporadic reproduction. Widely spaced forest fragments in a matrix of freshwater marsh coincide with the panther population that has been effectively extinct in the

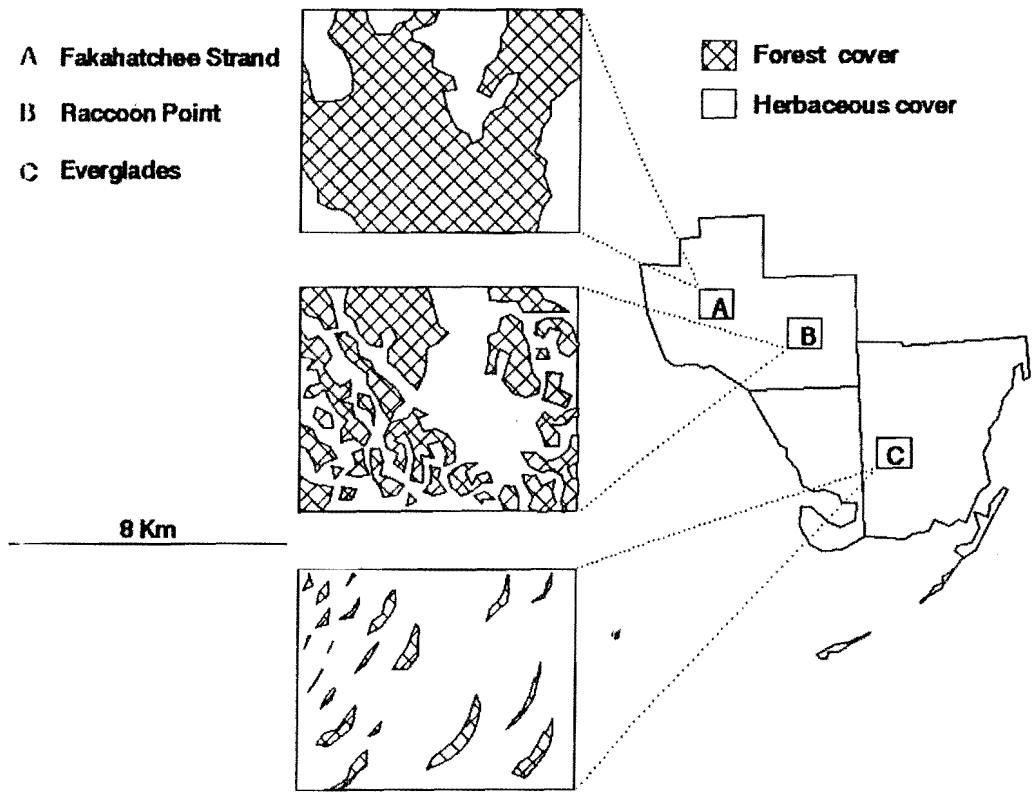


Figure 7.6. Northwest to southeast gradient of decreasing forest cover and increasing forest fragmentation in south Florida. Rectangular areas are approximately 50 km^2 and were drawn after U.S. Geological Survey (1993).

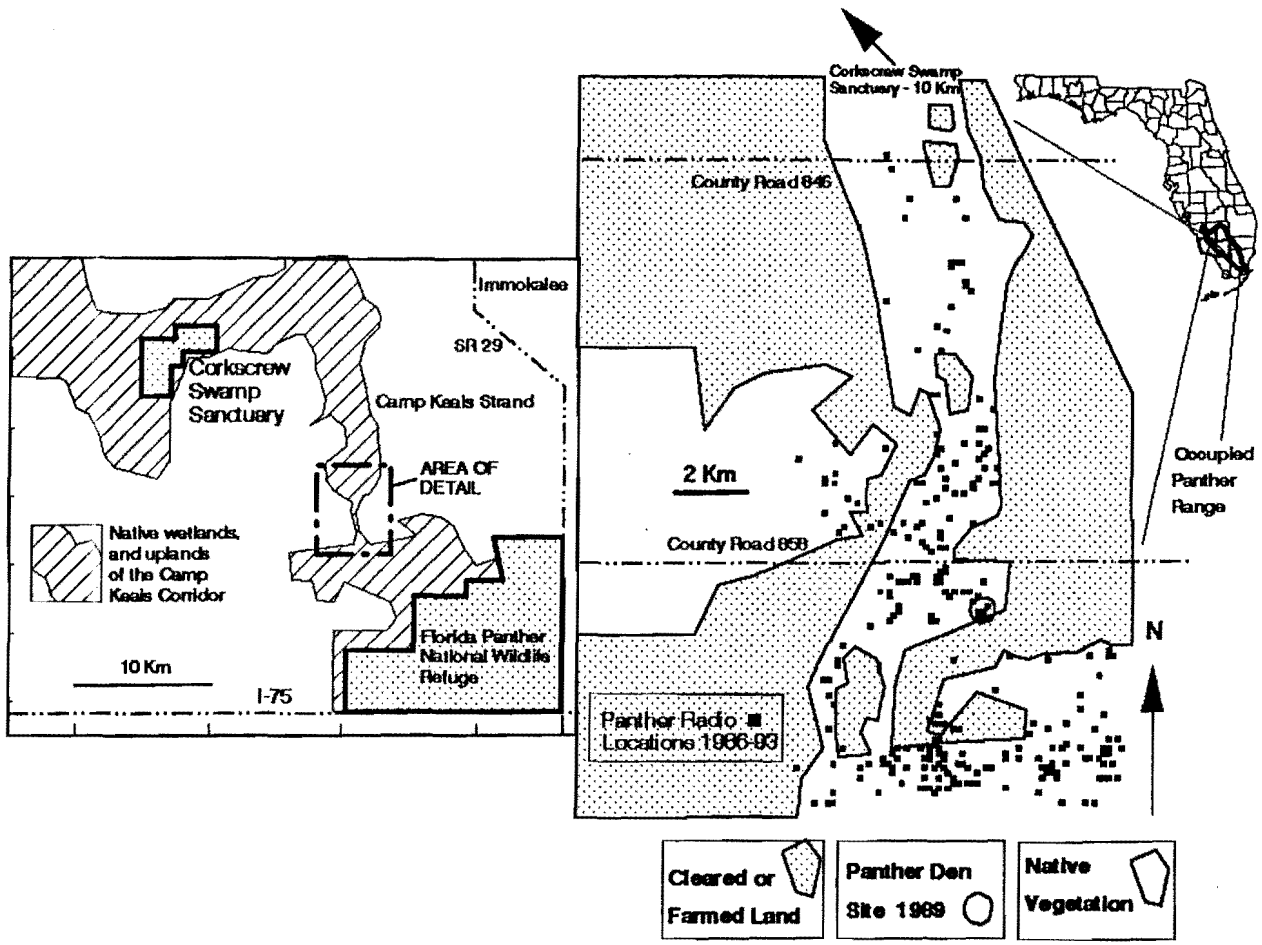


Figure 7.7. The Camp Keais Strand landscape corridor relative to major land features and the distribution of Florida panther radio telemetry locations.

Everglades since 1991. Patchy and fragmented forest cover is typical of most publicly owned land in south Florida.

Maehr (1990) observed that the loss of high-quality panther habitat on private lands to the north of the national park reserve complex would result in the loss of more than half of the existing panther population. Conversely, the loss of all National Park Service land in south Florida would result in only a minimal (<10%) population reduction - primarily the loss of individuals that contribute irregularly to reproduction. Thus, large preserve size is not, in and of itself, sufficient for the conservation of large carnivores, and successful conservation of these species depends on lands that are not owned by the public.

The coastal preserves of south Florida will be early victims of rising sea level (Henry et al. 1994), a phenomenon that has already caused reductions in freshwater forest systems (Craighead 1971). Before the advent of human landscape alterations such as canals, highways, and deforestation, wide-ranging mammals in south Florida were capable of following the gradual movements of plant communities as climate changed. Black bears are still capable of negotiating barriers such as the dredged, and channelized Caloosahatchee River and relatively large unforested areas (Maehr et al. 1988), but neither panthers nor bobcats have been observed doing the same. For bobcats, the demographic consequences of sea level rise with no escape route is less onerous because of their wide distribution and less extensive spatial requirements, but for panthers the impacts could be disastrous. All continuous upland connections between south Florida and points to the north have been dredged, cleared, impounded, farmed, or paved within this century.

However, corridors between south Florida preserves do appear to serve a local connecting function (Fig. 7.7). This suggests that if linkages between south Florida and south-central Florida were available, they would be used. Resident panthers routinely negotiate widely spaced forested upland and wetland systems. In some cases the connections between such ecosystems are no more than 100 meter-wide corridors of cypress that are bordered by farm fields and bisected by highways (Maehr 1990). These artificially narrow travelways vary in their use by mammalian carnivores: some serve as portions of home ranges while others act only as movement conduits (Fig. 7.7). The maintenance of these linkages will become increasingly important as changing environmental conditions compel populations to move.

Several studies suggest that black bears use corridors both for seasonal movements, dispersal, and protection from anthropogenic influences. Black bears use ravines, shelterbelts, canyons, and riparian strips to move within fragmented landscapes, feed, and escape harvest (Kellyhouse 1977, Beecham 1983, Klenner 1987, Mollohan and Lecount 1989, Weaver et al. 1990). Some authors suggest that black bear dispersal is simply a random process (Cox et al. 1994), but it is more likely that only the beginnings of bear dispersal are unpredictable, and that successful dispersers are those that follow some set of landscape gradients that facilitate safe travel. Female bear F16 demonstrated the possibility that landscape features influence carnivore distribution when she dispersed over 50 km in a single direction, paralleling Interstate 75 without crossing it. Although bears are capable of traversing unforested expanses, these individuals are susceptible to a wide range

of negative influences such as vehicles, dogs, intolerant home-owners, and anxious agency representatives.

As much as these species depend upon landscapes to support successful foraging for food, cover, and mates, they also provide landscape services or drive landscape processes that are often overlooked in traditional preserve design and management. Black bears in Florida are effective seed disseminators (Maehr 1984) and are likely important vehicles for conveying heavy plant embryos such as custard apple (Annona glabra), saw palmetto (Serenoa repens), cabbage palm (Sabal palmetto), and swamp dogwood (Cornus foemina) away from parent plants. The transport by bears of heavy-seeds such as saw palmetto may be an important aid to the plant's colonization of new, suitable range, and/or escaping deteriorating environmental conditions brought on by natural or anthropogenic causes. Further, the routine transport of seeds across the landscape may serve both plant and bear by facilitating genetic vitality in the plant, which, in turn, would help maintain the fitness of bears. Such mutualistic relationships have been demonstrated to be important evolutionary processes (Fleming 1992, Hunter and Price 1992).

Panthers do not exhibit the seasonal peregrinations that bears are prone to undertake, but their influence on prey species (Maehr et al. 1990) is likely just as important as bear herbivory and fruit predation. While defense mechanisms and dispersal characteristics of saw palmetto may have evolved under the influence of any number of Pleistocene foliovores and frugivores (i.e., giant ground sloth, Eremotherium spp.), the close distributional relations between North American deer (Odocoileus spp.) and Felis concolor is likely an example of predator-prey coevolution. While the black bear may be

no more than a surrogate for long-extinct Pleistocene seed eaters, panthers and white-tailed deer have changed together over evolutionary time in a predator/prey tug of war. That neither has succumbed in south Florida suggests that the process continues with both species exhibiting characteristics of "open program" genetics (Mayr 1976:696). The loss of the Florida panther would eliminate this process in eastern North America.

In the short term, most south Florida carnivore populations appear secure. The Florida panther, however, is threatened not only by the changes associated with expanding agriculture and more people (Maehr 1990), but by proposed short-term conservation actions (Maehr and Caddick 1995). The coyote will renew an old associative relation over the next few decades and exacerbate potential disease transmission already posed by domestic dogs and cats, but this potential problem pales with respect to other changes occurring at a global scale that threaten the long-range integrity of the carnivore community in south Florida. Nonetheless, management actions for Florida's carnivores have traditionally addressed short-term or symptom-oriented problems that will do little to ensure their long-term security. For example, black bear hunting in Florida was banned only after the result of citizen political pressure, and genetic introgression was initiated among Florida panthers despite the normal and productive demographics of the population (Maehr and Caddick 1995). Neither of these decisions have been followed by comparable efforts to protect the landscapes in which a growing bear population and a genetically "fortified" panther population could reside. Perhaps the only short-term management goal that warrants immediate action, and that is consistent with traditional wildlife management approaches, is the determination of the potential impacts of and controls for south

Florida's newest carnivore, the coyote. Developing an understanding of south Florida coyote ecology and instituting control programs at an early stage of the species' establishment may help buy time for the other carnivores that will increasingly be sharing their space and resources.

Clearly, a large area is required for evolution to continue among large mammalian predators and their prey, particularly when the potential for direct competition is minimal as is demonstrated by bobcats, black bears, and Florida panthers. It is unlikely that this process can continue in south Florida, however, without a way for panthers to evade an encroaching seascape. Given that the two existing very large preserves contribute insignificantly to the future of the Florida panther, and large terrestrial mammals in general, planning for these wide-ranging species must go well beyond the traditional approach of static-boundary nature preserves. The default non-action is to promote a further collapse in the ecological integrity of an increasingly depauperate and dysfunctional landscape system.

A discussion of the specific mechanisms to protect, manage, and restore south Florida as important large carnivore range is beyond the scope of this analysis, but the subject is not new. Maehr (1990) pointed out the importance of the private sector to Florida panther conservation, and Schortemeyer et al. (1991) detailed several approaches for managing a variety of landscape components to benefit this species. And, although key parcels of privately owned panther habitat were identified some time ago (Maehr 1991), no action has been taken to secure these areas nor have cooperative management plans been developed. The mechanisms for private land conservation have been known

and available for decades (Brenneman and Bates 1984), and yet large carnivore management in Florida has yet to evolve beyond the consideration of short-term effects. Enough is now known about the ecology of bobcats, black bears, and panthers in Florida to progress beyond the treatment of symptoms that stem from a larger dilemma.

APPENDIX A

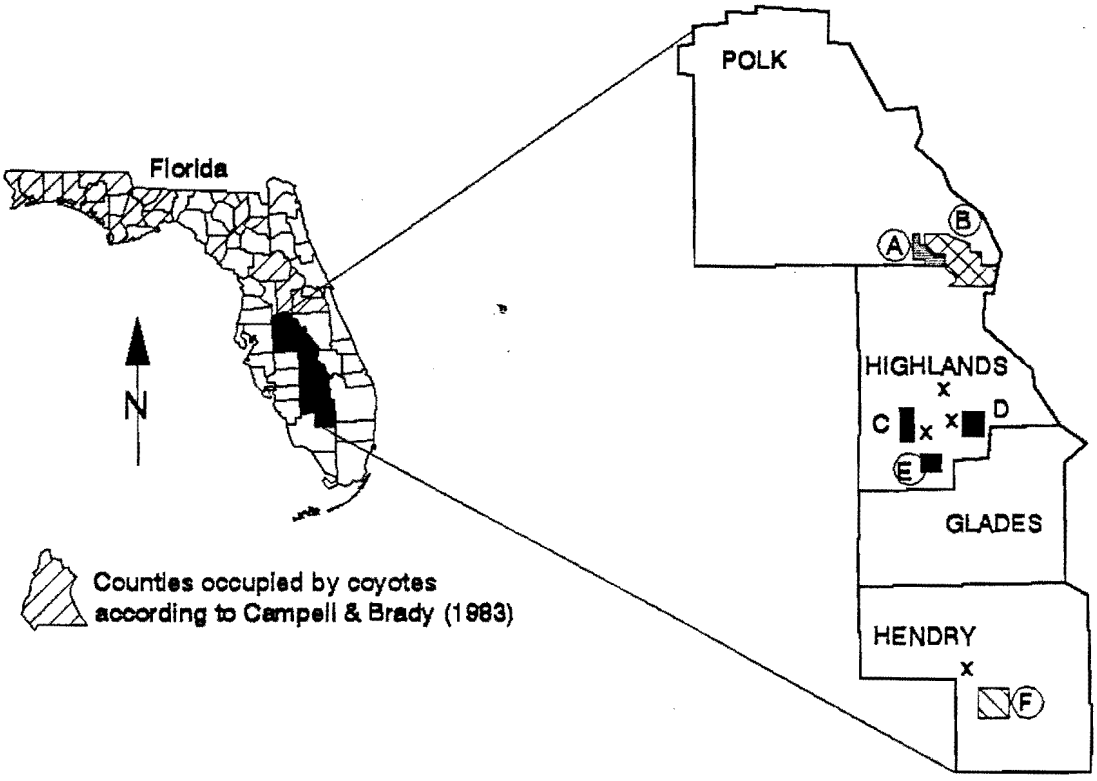
STATUS OF COYOTES IN SOUTH FLORIDA

Extensive changes in south Florida land use patterns have occurred since the early 1900s (De Bellevue 1976). Expanding agriculture has created a denatured landscape that is very different from pre-Columbian conditions. These expanses of large farm fields and fragmented forests have also created a new combination of wildlife species that have exhibited a variety of adaptive responses. Large mammalian carnivores such as Florida panthers (Felis concolor coryi), bobcats (Lynx rufus), and black bears (Ursus americanus) may benefit locally from some of these changes, but this less-forested environment has caused range-wide distribution contraction, population decreases, and increased anthropogenic mortality. Some of the beneficiaries of a drained and more open landscape include exotics with relatively small home ranges and generalist food requirements such as nine-banded armadillos (Dasypus novemcinctus), wild hogs (Sus scrofa), white-winged doves (Zenaida asiatica), and European starlings (Sturna vulgaris). The nomadic cattle egret (Bubulcus ibis) is likely the most abundant of these new immigrants. All of these species are numerous and obvious members of the new south Florida fauna.

A relatively recent, and little understood addition to this wildlife community is the coyote (Canis latrans). Although coyotes were introduced into south Florida as early as the 1920s (Hill et al. 1987), these individuals are thought to have disappeared (Brady and Campell 1983). In their review of coyote distribution, Brady and Campell (1983) doubted the presence of coyotes in south Florida, showing their occurrence in 18 mostly panhandle counties (Fig. A-1), whereas Wooding and Hardisky (1990:13) classified coyote occupation in south Florida as "scattered". Regular discoveries of coyote sign in Collier and Hendry counties began in 1989 during searches for Florida panthers (Roy McBride pers. observation), suggesting a recent expansion into south Florida. This likely is the result of changing land-use patterns and the coyote's ability to disperse great distances (>300 km) (Harrison 1992).

Following the elimination of several large mammals during the 19th century in the south central United States, coyotes inherited a landscape lacking the large native predators that evolved there. An animal community once dominated by the great plains grizzly bear (Ursus arctos), the plains wolf (Canis lupus), and the American bison (Bison bison), is dominated today by humans and domestic livestock. The modern coyote has no competitors except for man in most of its range. Its catholic diet and ability to increase in numbers despite predator control efforts have encouraged the spread of this medium-sized carnivore which now inhabits most of eastern North America.

Although coyotes have the potential to become livestock predators and probably compete with native wildlife such as bobcats, gray foxes (Urocyon cinereoargenteus), and panthers, the impact of this new Florida predator remains unstudied and undocumented. Additionally, coyotes can wreak havoc on valuable cash crops and other agricultural



A-1. Counties and locations searched for coyote sign from 3-18 June 1995. Circled letters represent locations where sign was found. Xs represent areas outside of formally searched properties where coyote sign was found. A=Arbuckle Wildlife Management Area, B=Avon Park Air Force Range, C=Archbold Biological Station, D=MacArthur Agro-Ecology Research Center, E=Hendrie Ranch, F=Hilliard Brothers Ranch.

produce. The presence of this highly adaptive and competitive carnivore has created a scenario for negative consequences not only on native fauna including the endangered Florida panther, but also on one of North America's most productive agricultural areas. With the exception of exotic plants such as Brazilian pepper (Schinus terebinthefolius) and melaleuca (Melaleuca quinquenervia), there are few non-native organisms that have the coyote's potential for becoming an economic and ecologic burden in south Florida.

When organized as a pack, coyotes are capable of capturing and killing wild ungulates such as white-tailed deer (Odocoileus virginianus) and elk (Cervus elaphus) (Robinson 1952, Ryden 1975, Moehlman 1989). Because of this, Lehner (1976:122) speculated that this represented "a predatory potential which might be more detrimental to livestock." Robel et al. (1981) observed that coyotes have been a major problem for sheep stockmen since the mid-1800s. Coyotes are also known to feed on other domestic animals including goats (Hawbecker 1939), poultry (Sampson and Brohn 1955), and cattle, especially calves (Hawthorne 1980). Cummings (1973) found that coyotes disrupted drip irrigation systems by chewing holes in plastic pipe, and coyotes can cause serious damage to watermelons and other fruit crops (Hawthorne 1980).

Generally, wildlife studies of non-game species are initiated when a problem has persisted for so long that the period of easy solutions has passed. In Florida, the panther exemplifies the consequences of delaying research and management. Recovery, if attainable, will only follow great public expense and acrimonious debate. It is possible that affordable coyote management in south Florida is still an attainable goal.

Hill et al. (1987) suggested that coyote "research efforts should document the nature and extent of impacts on wild fauna and agricultural commodities, and if appropriate, determine control methods compatible with the region's social values and land uses." A thorough understanding of coyote habitat requirements, food habits, and reproductive output in south Florida will be necessary to accurately evaluate the potential impact of this species on agriculture and native wildlife. This information will be needed to predict rates of population growth relative to available vacant habitat and their potential impact on competitors. These data could then be helpful in developing management recommendations to minimize crop and livestock depredations, and to avoid negative competitive interactions with native carnivores.

As a first step in better understanding coyote ecology in south Florida, a survey for coyote sign was conducted in south and south-central Florida. This represents the first effort beyond mail surveys to document the species' distribution in the south part of the state. The following summarizes the findings of a two-week survey that was conducted in south Florida in order to better understand the coyote's status and to determine if further study is feasible.

Study Area

Coyote sign was searched for throughout diverse landscapes that ranged from the southern terminus of the Lake Wales ridge to the northern drainages of the Big Cypress Swamp. Vegetative communities ranged from sand pine scrub, dry prairie, improved pasture, pine flatwoods, scrubby flatwoods, vegetable farms, and citrus groves. Descriptions of these native plant communities can be found in Myers and Ewel (1990).

Property ownership was predominantly private with the exception of an U.S. Air Force facility and a state wildlife management area.

Methods

I contacted by telephone owners of property >2000 ha to request permission to search for coyote sign using the technique described for Florida panthers by Roof and Maehr (1988). Coyote tracks and scats (feces) were looked for along unpaved roads, canal banks, fire breaks, and trails by walking or by driving a slow-moving all-terrain cycle or pickup truck. Locations of sign were recorded on area maps or on local highway maps.

Results and Discussion

Surveys were conducted from 3 through 18 June 1995. Not all contacted property owners granted permission for us to search for coyote sign. Thus, the findings presented here are a patchy representation of actual coyote distribution in south Florida. The key properties searched included the Avon Park Bombing Range (APBR), Arbuckle Wildlife Management Area (AWMA), Archbold Biological Station (ABS), the MacArthur Agro-Ecology Research Center (MAERC), the Hendrie Ranch, and the Hilliard Brothers' Ranch (Fig. A-1). Public roads adjacent to properties in southern Highlands County, especially those with access to citrus groves, were also searched. Time constraints precluded searches on other private lands such as the Scofield Ranch in Collier County and the Smoak Ranch in southern Highlands County.

Southern Polk County/Northern Highlands County- Coyotes were present in both the Polk County and Highlands County sections of APBR. The highest concentration of sign was found in the north-central portion of the range, but evidence of coyotes was encountered

throughout the property. Records maintained by APBR personnel indicated that coyotes have been seen on the range since 1970 but that they appear to be concentrated in the center of the facility (P. Walsh pers. comm.). This survey suggests a more widespread distribution of coyotes than sightings alone would have indicated. The AWMA provided sparse evidence of coyotes. However, because it is contiguous with APBR, the individuals using Arbuckle are likely residents of both areas.

Southern Highlands County- Neither ABS nor the MAERC contained sign of coyotes, however coyotes have been seen by the ranch manager on the latter property (J. Mullahey, pers. comm.). In addition, tracks were found on adjacent properties; immediately to the west of MAERC, immediately east of ABS, and just north of State Highway 70. In these cases coyote sign was associated with citrus groves. This was the same area that was frequented by a Florida panther before its capture and instrumentation in 1988 (Layne and Wassmer 1988, Maehr et al. 1992). The duration of this survey was insufficient to conclude that ABS and MAERC are not used by coyotes; it is more likely that coyotes have not yet become permanent residents in these areas because sign was found in similarly vegetated areas such as AWMA and APBM. The relatively open nature of MAERC and the relatively heavily vegetated ABS are land cover extremes, but they are both used by coyotes elsewhere.

Coyotes were implicated by a local rancher in the deaths of over 200 sheep near Venus, Florida during 1993 and 1994 (J. Hendrie, pers. comm.). While they may not have been responsible for all of these losses, the presence of their sign on and nearby the Hendrie Ranch suggests that coyotes certainly have the opportunity to prey on a domestic

species that is consumed by conspecifics throughout their range. Generally, coyotes cause more sheep losses than any other predator in the western states where dollar losses in an individual state can exceed 3 X 10^6 (Bekoff 1982).

Southern Hendry County- Although only one area was searched in Hendry County, anecdotal evidence suggests that coyotes are widespread throughout the sections of the county that contain improved pasture and other agricultural activities. In addition to frequent sighting reports, and reports of harvested animals, I documented coyote tracks at the edge of a vegetable farm near Felda, Florida during November 1994. This survey turned up abundant sign on Dinner Island where improved pasture dominates the landscape. This area originally supported extensive pine flatwoods and a combination of isolated wetlands and the large north-south-flowing Okaloacoochee Slough before the uplands were cleared for agriculture. Surrounding properties (where permission to survey was unobtainable) are very similar in terms of vegetation and land use, and likely support comparable numbers of coyotes as exist on Dinner Island.

Despite the inability to conduct an uninterrupted survey throughout south Florida, the consistent discovery of coyote sign in most areas examined suggests that coyote distribution from southern Polk County through Hendry County is interrupted only by the Caloosahatchee River. Lack of access to property in Glades County precluded surveys in this relatively unpopulated area, however, the combination of extensive improved pasture and remnant forests has created a milieu very similar to occupied range to the north and south. Contrary to the conclusions by Campell and Brady (1983) and Wooding and Hardisky (1990), this survey revealed that southern peninsular Florida contains a large

area that is permanently occupied by coyotes. This difference may have resulted from biases inherent to mail surveys, or it may reflect a change in the coyote's status since the earlier papers were written. Evidence supporting range expansion is provided by APBR natural resources staff (P. Walsh pers. comm.) and suggests a dramatic increase in coyote sightings since 1970. In addition, three coyotes were harvested on APBR after 1992, and Mr. James Hendrie reported significant depredations on sheep only within the last two years in southern Highlands County.

With the exception of their apparent expanding range, little can be inferred about coyote ecology in south Florida. Three scats from APBS contained native plant and animal remains, and they were collected in an area that is an active livestock range. Although there is some evidence that coyotes in Florida are a significant predator on livestock, abundant native prey species likely reduce the potential for depredations. Nothing has been reported on coyote den and food requirements in Florida, however, H. W. Kale, II (pers. comm.) observed a coyote family within a dense saw palmetto (Serenoa repens) thicket in the phosphate region of central Polk County, and S. Seibert observed coyote scats composed of saw palmetto seeds in Apalachicola National Forest. This plant is commonly used by all of south Florida's native mammalian carnivores for food, cover or both.

Until the 20th century, Florida supported permanent populations of native canids that included gray fox, and red wolf (Canis rufus) (Robson 1992). Although it could be argued that the coyote has simply filled vacant niches of extirpated congenerics, the loss of the red wolf coincided with the clearing of forests that have been replaced by agricultural

lands and urban centers. As a result, Florida has become an increasingly open, range-like state that is more similar to the native range-lands of western North America that are considered typical coyote habitat. Thus, the coyote's niche in Florida is a relatively new one. The presence of the coyote in Florida today is a symptom of regional faunal collapse resulting from the fragmentation and denaturization of the landscape. Based on food habits studies in other parts of their range, coyotes have a greater potential to overlap with Florida's three large native mammalian carnivores than panthers, bears, and bobcats currently overlap with each other. With sufficient fragmentation of native forests that these native species prefer, coyotes may compete with black bears for mast such as blueberries (Vaccinium spp.), gallberries (Ilex glabra), saw palmetto), with bobcats for small mammals (rodents, rabbits), and with panthers for medium- and large-sized prey (nine-banded armadillos, wild hogs, white-tailed deer).

Conclusion

This survey confirmed the presence of coyotes from the southern Lake Wales Ridge to the northern Big Cypress Swamp. The variable abundance of sign suggests that coyotes exhibit inconsistent rates of occupation. This may be the result of differences in habitat quality, inconsistent survey efforts, or may be a reflection of the coyote's continuing range expansion. In any event, the distribution of sign was sufficient to be the product of a population that exists in numbers that could support intensive study including radio telemetry. This work would prove valuable in determining the potential for coyotes to impact native carnivores, farmers, and ranchers, and for developing methods of coyote control in the new south Florida canid niche.

competition, prey size, and environmental productivity were the primary factors affecting body size in mammalian carnivores. I examined measurements of mass in Florida black bears (Ursus americanus) and Mexican black bears (Doan-Crider and Hellgren 1996) in order to better understand the effects of these variables on black bear mass growth.

Study Area and Methods

The south Florida study area, at approximately 26°10' N, 81°35' W, is within a flat, humid, forested landscape with tropical savannah climate (Hela 1952). Elevation varied from 0 to 20 m above mean sea level (MSL). The northern Mexico study area, at 28°40' N, 102° 15' W, is within a rugged, mountainous landscape that varies from 1400 to 2100 m MSL. Vegetation associations vary from chaparral grasslands to montane mesic forests, depending on elevation, slope, and aspect (Doan-Crider and Hellgren 1996). Mean annual temperatures are 23° C and 16° C for Florida and Mexico study areas, respectively (Deuver et al. 1986, Doan-Crider and Hellgren 1996). Rainfall averages 67 cm in northern Mexico and 150 cm in southern Florida (Duever et al. 1986). Both study areas experience extended dry seasons, with peaks in rainfall occurring during summer.

Black bears were captured in Aldrich spring-activated snares (Aldrich Snare Co., Clallam Bay, Washington) or in culvert traps (Erickson 1957), before they were anesthetized with Telazol (Doan-Crider and Hellgren 1996) or ketamine hydrochloride according to dosages in Maehr et al. (1989). Mass measurements were obtained with a kg-graduated spring scale (Doan-Crider and Hellgren 1996), or with a pound-graduated spring scale. The latter measurements were then converted to a metric standard. Ages were assigned in the field if cub sizes suggested they were young-of-the-year, or they were

determined by evaluating cementum annuli from an extracted first premolar (Matson's Laboratory, Milltown, Montana).

Recaptures of bears were eliminated from analyses to expunge a source of error autocorrelation. In addition, only captures from April through October of free-ranging bears were used to minimize the potential for winter captures of Florida bears to bias comparisons between areas. Because Maehr and Moore (1992) observed that neonate mass measurements would increase the precision of the model, and because black bear birth mass seems uninfluenced by gender or geography (Pelton 1982), mass measurements of Mexican female cubs handled during March were used to anchor the origin of growth curves near a realistic starting point. Mass was plotted against age by cohort (all bears of the same gender from one study location), and the Richards model was used to develop the curve (Brisbin et al. 1986, Leberg et al. 1989):

$$M(t)=\{A^{1-m} - [A^{1-m} - B^{1-m}] \cdot \exp[-2t(m+1)/T]\}^{1/(1-m)},$$

where M(t) represents mass at age t (months), and A and B are asymptotic or adult mass and birth, respectively, and T represents the time period required to complete the "major part of growth" (Richards 1959:298). Model selection criteria are described in greater detail by Maehr and Moore (1992). Curves were fit only for cohorts that exhibited data convergence (PROC NLIN; SAS Institute, Inc. 1988).

Results and Discussion

Captures of individual black bears totaled 59 (29 females, 30 males) in south Florida, and 62 (21 females, 41 males) in northern Mexico, however, not all measurements

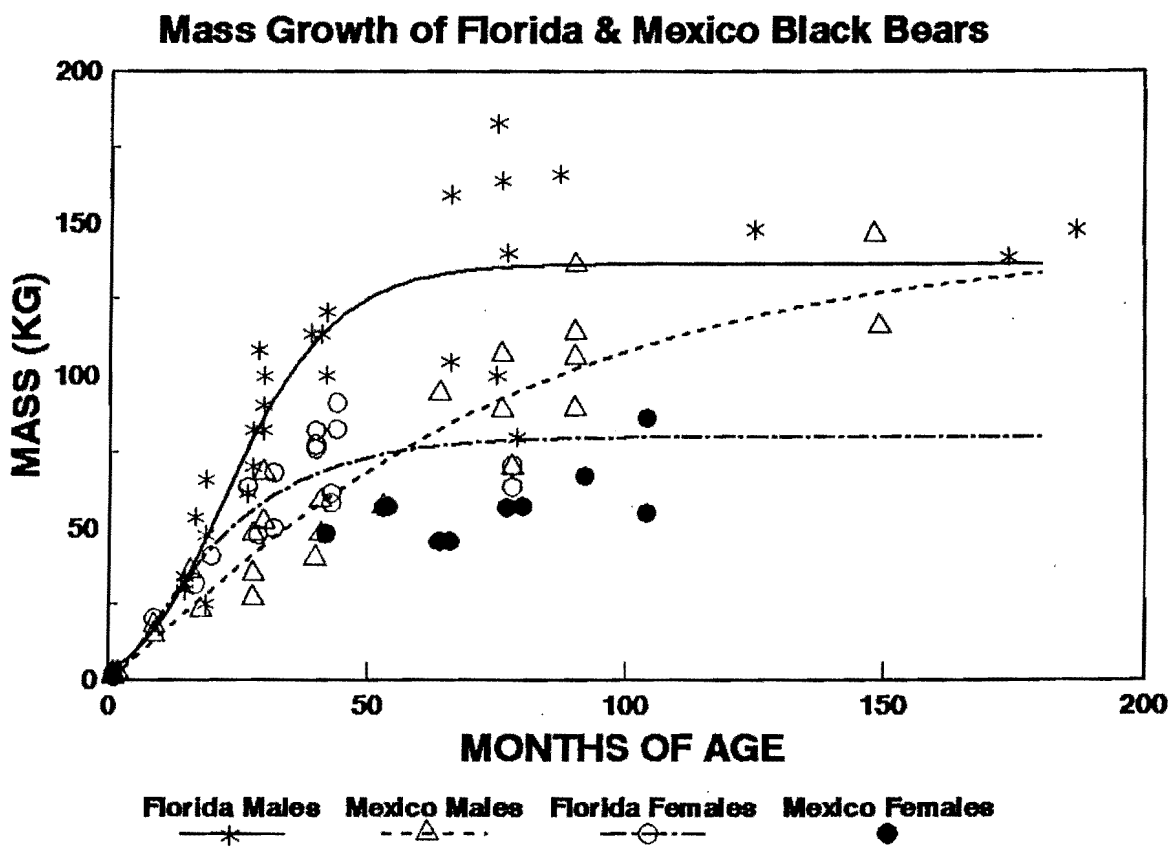
Table B-1. Sample size, R^2, point (θ), and interval (ASE) estimate of parameters from Richards growth curves fit to $\log_e$, mass data from 2 wild black bear populations.

				A(kg)		T(months)		m		B(kg)	
Population	Sex	n	R^2	θ	ASE	θ	ASE	θ	ASE	θ	ASE
Florida	M[a]	30	0.78	136.6	11.2	53.6	10.4	1.32	2.08	3.93	14.48
Florida	F[b]	21	0.89	80.1	7.0	47.9	9.2	0.43	0.26	0.19	0.40
Mexico	M[a]	41	0.94	144.2	41.6	152.0	65.6	0.17	0.18	0.52	0.42
Mexico	F[b,c]	18	-	-	-	-	-	-	-	-	-

[a]Sample obtained from April-September
[b]Sample obtained from April-October
[c] PROC NLIN (SAS Institute, Inc., 1988) failed to converge point data

Table B-2. Z-values and probabilities for paired comparisons of asymptotic mass (A), time to adult mass (T), and growth curve shape (m) for 2 wild black bear populations.

Population pair	Parameter	Z-value	Probability
Florida male v Florida female	A	3.37	0.0004
	T	0.0296	0.488
	m	0.2024	0.421
Florida male v Mexico male	A	0.176	0.428
	T	1.4819	0.069
	m	0.550	0.2912



B-1. Patterns of mass growth in Florida and Mexico black bears based on the Richards curve.

were used. Mass ranged from 2.2 to 146.0 kg for Mexican males (age=4-148 months), from 1.0 to 86.0 kg for Mexican females (age=1-104 months), from 29.5 to 147.7 kg for Florida males (age=15-187 months), and from 20.4 to 90.9 kg for Florida females (age=9-116 months).

The sample size was insufficient to fit a curve to the data collected from Mexican females, so these data are presented in Figure B-1 only as individual symbols. Asymptotic mass was higher ($P<0.001$) for Florida males than for Florida females, but there was no difference between males from Florida and Mexico (Table B-1). Although same-gender cohorts from both populations attained similar adult mass (A), individuals from Florida tended to reach this asymptote (T) sooner ($P=0.07$) than those from Mexico (Table B-1). Mass growth has been correlated with age at first reproduction in black bears (Bunnell and Tait 1981, Rogers 1987a), thus, individuals from Florida should be expected to begin breeding at an earlier age than those in Mexico. Indeed, females in Florida consistently experienced their first estrous at 2.5 years- the earliest age reported for the species. In Mexico, age at first reproduction for three females averaged 4.5 years (Doan-Crider and Hellgren 1996). In most areas where black bears exhibit an early age of first female reproduction, a high nutritional plane is implicated as the causative effect (Pelton 1982, Schwartz and Franzmann 1991).

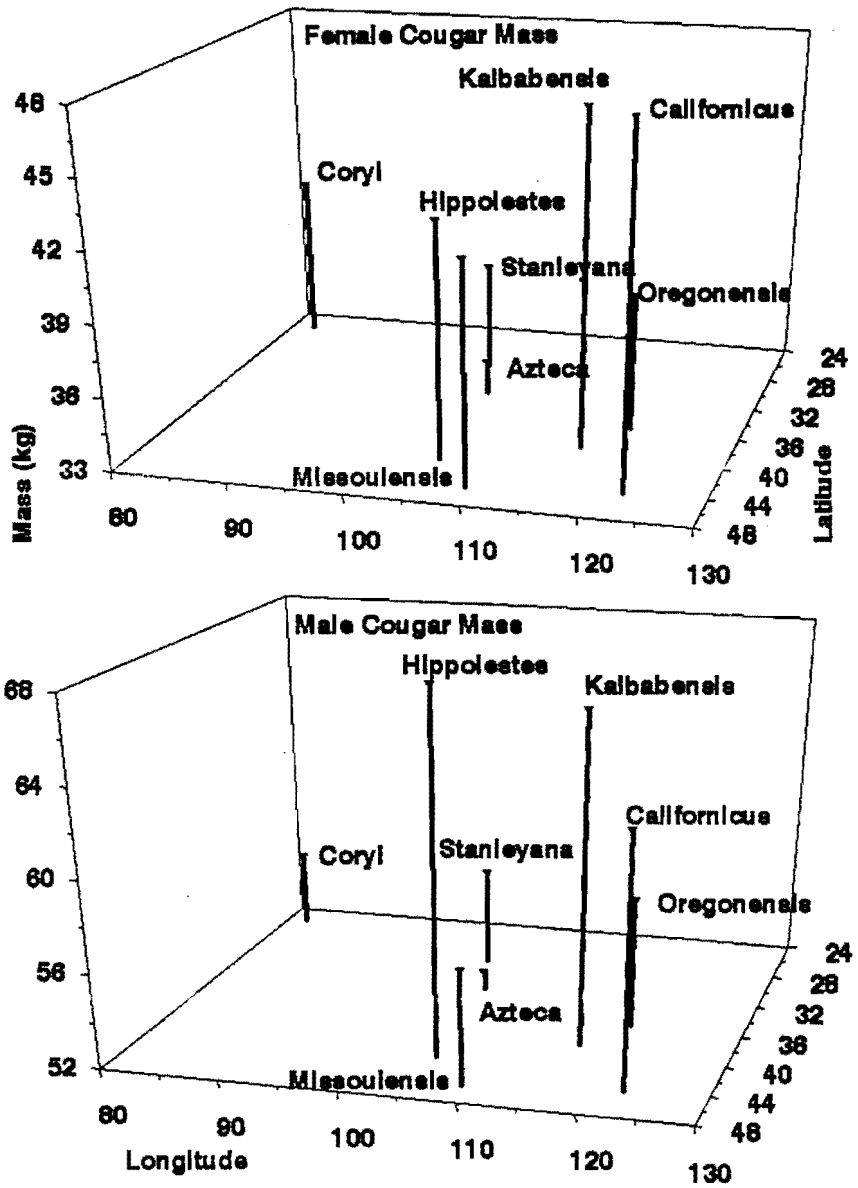
The year-round availability of nutritious foods in south Florida (see dietary overlap chapter) may not only explain winter activity among individuals, but also early breeding capacity of females and rapid growth in both sexes. In most parts of the species' range, all individuals regardless of gender, reproductive status, and age, den for four to seven

months (Pelton 1982). Although male bears in Mexico remained active during winter, denning females were approached and handled (Doan-Crider and Hellgren 1996) with greater success than those in Florida, which remained alert and ambulatory during winter at natal dens. Because of this behavioral difference, no adult females were handled at their dens in Florida. Warmer winter temperatures in Florida may prevent bears from entering the deep hibernation that is characteristic of more northern or higher altitude populations (Nelson and Beck 1984). It is of interest that some Florida males exhibited denning behavior by building ground nests and remaining at a single location for more than one week, but these individuals remained alert and fed on local vegetation throughout the winter. Comparable food habits data were not available for both study areas, however south Florida supports several native and introduced plant species that provide high-energy, high-digestibility foods throughout the winter (see dietary overlap chapter). In the Mexico study area, several oak species were abundant, and if sufficient mast crops were produced, these may provide winter food for males if competition with other acorn predators is minimal. As is characteristic of oaks in most parts of their range, however, acorn production follows cycles of abundance and scarcity that are not always predictable.

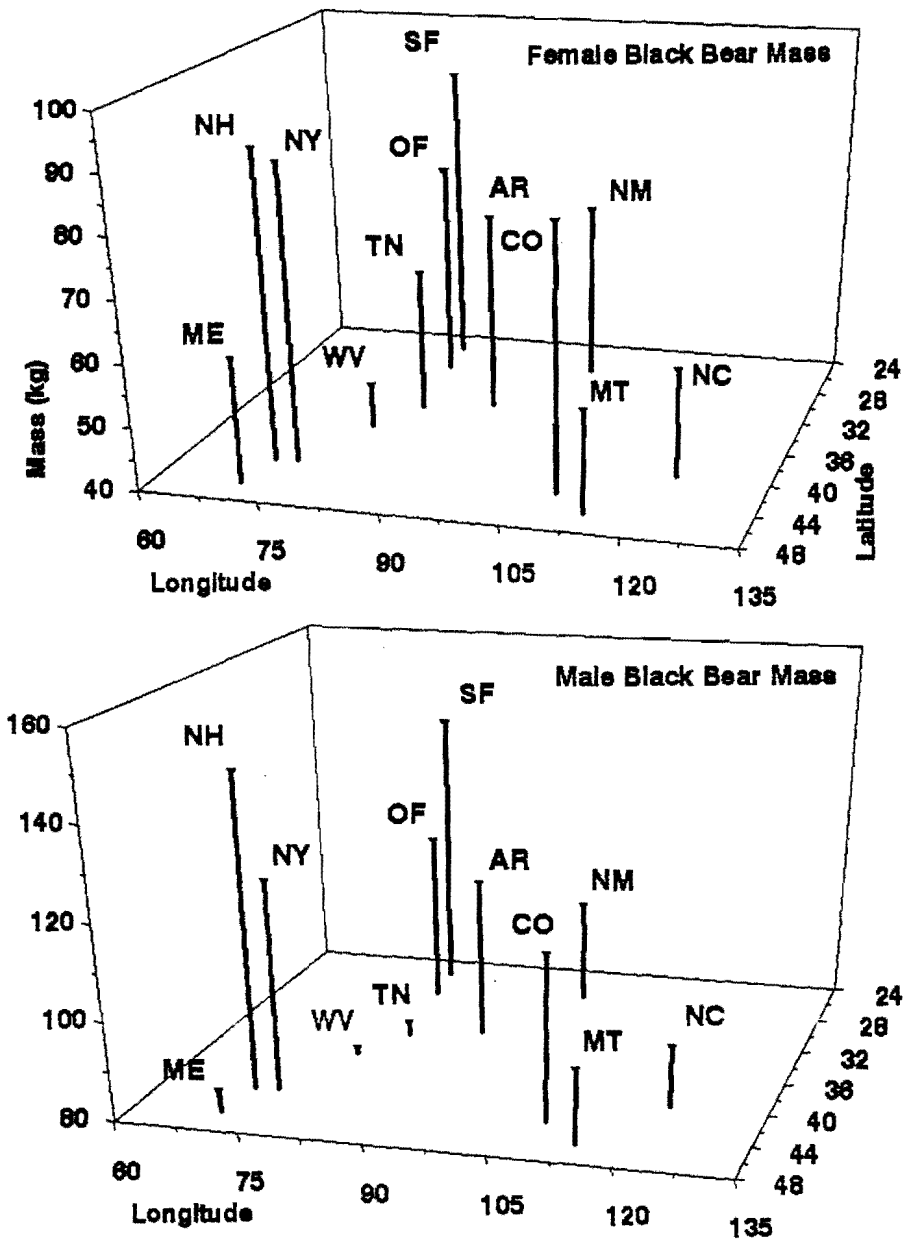
It has long been observed that Florida black bears do not exhibit a tendency toward smaller mass when compared to conspecifics from northern latitudes (Harlow 1961). Although over-winter mass reductions have been observed in south Florida, the annual period of negative foraging is clearly much shorter than in populations from temperate climates. For example, the denning period for Florida females is 33% shorter than that reported for Mexican females (79 v 118 days, respectively). Although no male

denning was reported in Mexican males, occasional bouts of dormancy may have gone unnoticed due to less frequent radio-monitoring. Denning Florida males frequently left their dens or occasionally relocated these sites throughout the winter. In south Florida winter activity may be advantageous from several perspectives. For solitary females, a higher nutritional plane may speed maturation in younger animals and may encourage consistently larger litter sizes (or reduce reproductive failures in alternate years). Among males, a shorter or less severe negative foraging period may allow them to reach breeding condition earlier, and maintain good physical condition through a longer breeding season. Simply put, Florida black bears may grow faster than other populations of the species because they lose less weight for a shorter period of time than elsewhere.

Although Geist (1987) previously invalidated Bergmann's rule, variation in North American black bear mass would be compelling evidence against its universal applicability. The uniquely tropical south Florida population provides the strongest argument against an over-arching latitude and mass relationship among mammals, and suggests that there are factors other than latitude that influence mass growth in carnivores. If one examines mean weights of cougars in North America, it is difficult to refute Bergmann's rule if increasing altitude is considered analogous to more northern latitudes. Thus, geographic variation in cougar mass (Fig. B-2) can be reconciled by noting the correlation between larger mass and western mountain ranges. When similar data are viewed for black bears (Fig. B-3) there is no easily explainable trend in body mass for either gender, and altitude does not seem to influence continental black bear mass patterns. Populations from New England and Florida exhibit the highest values, whereas populations from the central Appalachians exhibit the smallest. As one proceeds west from Florida, mass declines to moderate levels



B-2. Effect of geography on cougar mass in North America.



B-3. Effect of geography on black bear mass in North America. OF=Ocala National Forest, SF=South Florida; others are standard two-letter state abbreviations.

in mountain and Pacific coast areas. Although bears from Mexico and Florida are from similar latitudes, and grow to similar mass, Mexican bears require three-fold more time to attain asymptotic mass. The lack of a consistent and explainable geographic trend in black bear mass may be the result of inconsistencies in the way these measurements were reported and categorized. Variation in the inclusion of different age classes may strongly influence means for individual studies. This was not the case, however, in the comparison between Mexico and south Florida, so I suggest that the observed differences in mass growth are directly related to the climate and productivity of the study areas.

Although climate cannot be considered a landscape feature per se, it is often a product of continental geomorphology, an underlying cause of landscape pattern (Zonneveld 1990). For example, virtually every other continental land mass at the same latitude as peninsular Florida is a desert (Ewel 1990). The peninsula's position within the warm Gulf Stream allows tropical and humid conditions to prevail for most of the year. Even during the dry season, abundant subsurface waters are available to a diverse flora that subsists in sandy soils (Ewel 1990). While soil productivity in northern Mexico is likely much higher than in southern Florida, semi-arid conditions limit the availability of these nutrients to only the hardiest plant species. This is a pattern common to tropical areas with low rainfall, higher-altitude, and lower temperatures (Eisenberg 1989:432). As a result, Mexican winters create a situation more like an extended annual drought than the rainless, but moist conditions that can persist throughout the year in parts of south Florida that have yet to be artificially drained. In south Florida, abundant water resulting from the positioning of the landscape moderates climate and encourages the luxuriant plant growth

that drives black bear mass growth: a rate that may be paralleled elsewhere in the species' range only in some very productive parts of Pennsylvania (Alt 1980). That Florida panthers and other carnivores do not also exhibit a similar trend seems to be related to some of the factors suggested by Rosenzwieg (1967) as controllers of carnivore body size.

For black bears, latitude alone is insufficient to explain continental variation in mass, and prey size is irrelevant because most of their diet is composed of plant matter. The limits to mass growth rate in Mexican black bears may be related to competition with other seed eaters, lower mean temperatures, and environmental productivity that is limited by an arid climate. All of these factors are interrelated, but temperature and nutrition seem to be the factors that are most likely to explain a pattern of mass growth that otherwise appears totally confounded with other variables. In this sense, the primarily vegetarian black bear is much more a product of the landscape and local environmental conditions than panthers and other obligate meat eaters.

APPENDIX C

FLORIDA PANTHER POPULATION GROWTH

A recent review portrayed the Florida panther (Felis concolor coryi) as demographically reduced and genetically depleted (Roelke et al. 1993). Although the panther's genetic variability is indeed reduced relative to conspecifics, it is greater than that exhibited by cheetahs (Acinonyx jubatus) (O'Brien et al. 1987), and is within the range exhibited by many mammalian species (Nevo et al. 1984 cited by Caughley and Sinclair 1994:247). Contemporary discussions of Florida panther conservation biology such as Hedrick (1995) frequently cite the interpretation of an outdated population model originally presented by Seal and Lacy (1989) despite the availability of more recent information (i.e. Maehr et al. 1991a, 1991b). As a result, the panther is the subject of demographic deflation, and management decisions have subsequently been made (Jordan 1993) to address a problem that is much worse than is exhibited by the south Florida population.

Mathematical population models are useful for identifying biological information gaps and in suggesting parameters that influence population growth. However, because these models are abstractions of complex biological systems, care must be exercised in their application. For example, Lande (1988) identified two management plans that, if

implemented, would threaten the existence of the species they were intended to help because basic demographic factors were ignored.

The Florida panther recovery plan (U.S. Fish and Wildlife Service 1987) was substantially altered after the application of VORTEX, a population simulation program designed after Grier (1980, cited in Seal and Lacy 1989), that predicted "extinction in 25-40 years due to genetic and demographic factors" (Seal and Lacy 1989). This resulted in the removal of 10 wild-born panther kittens in order to form the nucleus of a captive population. Previous to this, a simulation model developed by C.L. Abercrombie (1987, unpub. report to the Florida Game and Fresh Water Fish Commission) predicted an equally pessimistic future for the panther, but was shelved due to unreliable and purely speculative population parameter estimates. More recently, the VORTEX simulation was used to justify genetic introgression of Florida panthers (Seal 1992). The development of both simulation models depended on a number of assumptions relative to population demographics because field studies of free-ranging panthers still were uncovering basic biological parameters. This paper reexamines Abercrombie's 1987 model using the most recent biological data available and compares it with the VORTEX simulation.

Methods

The model is a modified Leslie matrix written in BASIC that partitions a population of 50 individuals into three vectors: males, females with kittens, and females without kittens. Based on the observed demographic characteristics of and spatial overlap among individuals in the population (Maehr et al. 1989a, 1991a, 1991b, Maehr and Caddick 1995, and Florida Game and Fresh Water Fish Commission unpubl. data), the

model restricts maximum age to 15 years, allows a single adult male to service up to three adult females, permits litter sizes to range from zero to four (with a neonate sex ratio of 1:1), uses an adult sex ratio of 3:1, and an interbirth interval for adult females of 24 months. The model is designed to be altered by the user in order to change values of individual demographic variables so that the importance of a single variable can be better understood. Specifically, the number of simulation-years can vary (I used 100 years throughout). A size limit which the population can not exceed can be specified or the population can be left to grow without limit. The probability of a complete failure in annual reproduction can be set (a value bounded by 0 and 1), and a discrete probability distribution of litter sizes can be specified (total of all probabilities must equal 1).

In addition, the model's user can determine whether or not the population is affected by density dependence, a variable that clearly oversimplifies such a complex ecological process. If density dependence is selected, then the survival of kittens aged zero to 12 months of age is affected by the algorithm $S=0.8-0.3(N/K)$ where N is the total population for a given simulation year, K is the user-selected carrying capacity, and S is the density dependent kitten survival rate. The value 0.8 is the default kitten survival rate and 0.3 is an arbitrary linear reduction constant. In situations where N exceeds K, the value of S is constrained so that it is always greater than or equal to 0. Further, because intraspecific aggression among males is the most common form of natural mortality (Maehr et al. 1991b), successful recruitment for subadult males between one and three years of age is constrained by the model. If a vacant adult male home range is available for a subadult male to move into, then the survival probabilities for one-year-olds and two-

year-olds become 0.8 and 0.85, respectively, until that vacancy is filled; otherwise they remain at 0.2 and 0.25, respectively.

In instances where an entire litter is lost, the mother of that litter is returned to the potentially reproductive vector. The program limits the total number of potentially pregnant females to three times the number of adult males. Survival for individuals within a population cohort are determined by "coin-toss". For example, if survival of four-year-old males is 0.6, then for each animal in that cohort, the BASIC random-number generator selects a number from a uniform distribution that is limited by zero and one. If that number is less than or equal to 0.6 then that individual lives through the simulation year. If the number is greater than 0.6 then that individual is expunged from the population.

When all user options have been exercised, the model runs for the specified number of years, and then the entire simulation is run 500 times. Printout results summarize the average population size and standard deviation (across the 500 runs) at the end of 100 years, and the probability that the population persists for this time period.

Results and Discussion

Clearly, the ability of a population to maintain itself or increase is dependent upon successful reproduction. As total annual kitten production approached the rate indicated by observed litter sizes, persistence probabilities approached 0.90 (Fig. C-1). This was true even for model runs where the combined likelihood of litters greater than two was 0.30 (Table C-1). Increases in the frequency of larger litters did little to add to persistence likelihood. Kitten survival, on the other hand, had dramatic effects on potential population size and persistence probabilities when growth limits were removed (Fig. C-2). At kitten

Table C-1. Effect of litter size probability on Florida panther population persistence for 100 years[1].

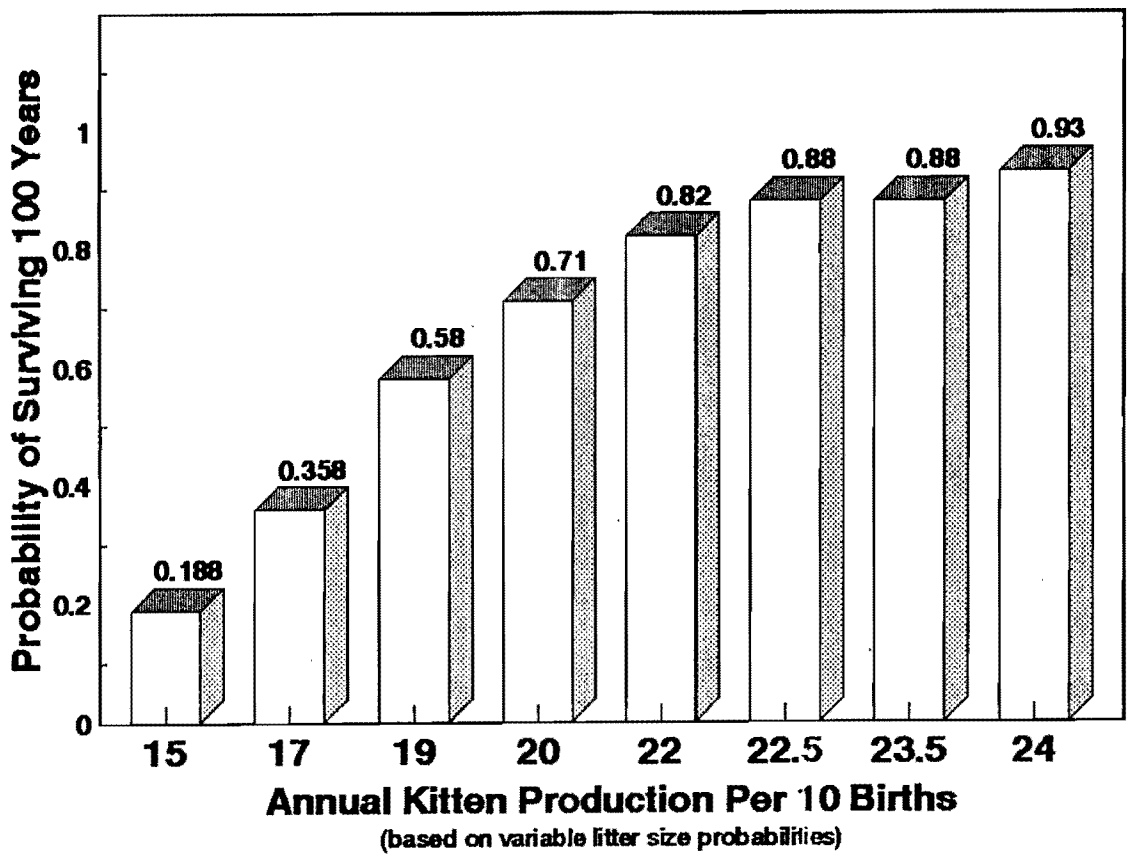
Litter Size Probability						
0	1	2	3	4	Probability of survival	Mean population after 100 years (SD)
.15	.35	.35	.15	.00	.188	12.31 (6.48)
.10	.25	.50	.15	.00	.358	16.35 (9.02)
.05	.25	.50	.15	.05	.580	21.68 (10.89)
.05	.20	.50	.20	.05	.710	24.09 (12.16)
.00	.15	.55	.25	.05	.820	31.58 (13.12)
.00	.10	.60	.25	.05	.880	30.30 (13.62)
.00	.10	.50	.35	.05	.880	31.56 (12.94)
.00	.10	.50	.30	.10	.930	38.60 (13.64)

[1] Population size was limited to 70, default adult survival, kitten survival=.80, chance of annual reproductive failure=.10, carrying capacity=60 (SD=10), survival of subadult males dependent upon home range vacancies.

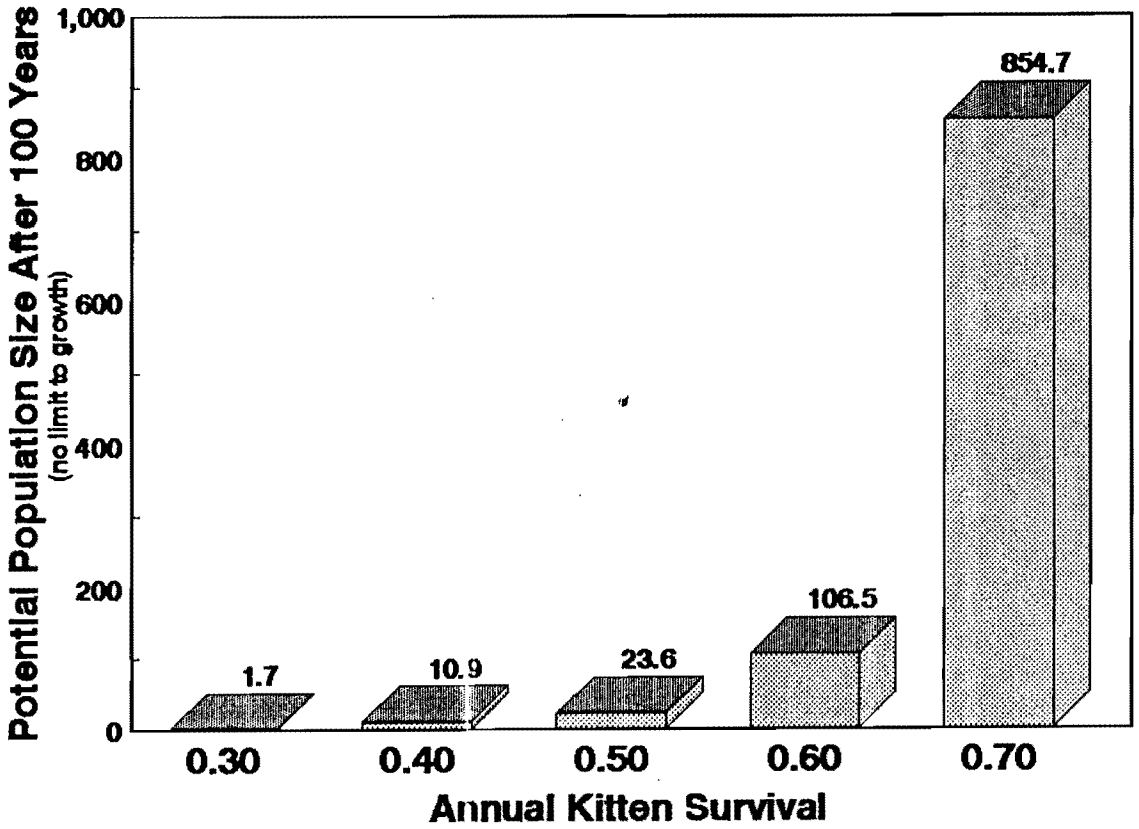
Table C-2. Effect of kitten survival on Florida panther population persistence for 100 years[1].

Kitten survival rate	Probability of persistence	Mean population after 100 years (SD)
.30	0.0	1.7 (0)
.40	0.054	10.9 (7.01)
.50	0.436	23.6 (15.27)
.60	0.942	106.5 (75.2)
.70	1.0	854.7 (522.63)

[1] No arbitrary population limit, default adult survival, default litter sizes, no reproductive failures, no density dependent mechanisms.



C-1. Effect of litter size probability on Florida panther population persistence for 100 years.



C-2. Effect of kitten survival on Florida panther population persistence for 100 years.

survival rates of 0.60, the probability of persistence exceeded 0.94 (Table C-2). Thus, when other variables were held constant, observed mean litter size and observed kitten survival rates were at least adequate to maintain model populations at numbers within the range of current estimates (Table C-1), and have the potential to allow dramatic increases given the availability of adequate space.

The possibility of periodic annual reproductive failures is one of many variables that may affect the persistence of small populations (Boyce 1992). While this aspect of demographic stochasticity has not been observed in Florida panthers, the Abercrombie model suggests that the probability for such an event must exceed about 0.20 to reduce the population survival probability below 0.80 (Fig. C-3). Even with a 0.10 probability of annual reproductive failure, model populations maintained a 0.98 probability of persistence when demographic characteristics reflecting observed values were used (Table C-3).

The critical range for adult survival fell between 0.70 to 0.75 (Fig. C-4). At a survival rate of 0.76, the model calculates a 0.97 probability for the population to survive 100 years. On the other hand, at 0.70 and below no simulated populations survived. Although the population exhibits adult survival that exceeds this threshold (Maehr et al 1991b), a uniform survival rate of 0.80 from one to 14 years of age does not impart any advantages to the modeled population even though the mean survival rate is higher than the mean for all ages in a variable survival rate distribution (Table C-4). The most successful combination of adult survival rates was one that exhibited 0.80 to 0.90 survival among adults aged five to nine years of age, lower survival probabilities for younger and older males, and slightly reduced survival in older females. Run 4 of Table C-4 exhibits adult characteristics typical of Florida panthers, and is the most representative of survival

Table C-3. Effect of frequency of reproductive failure on Florida panther population persistence for 100 years[1].

	Probability of population-wide annual reproductive failure					
	0.50	0.40	0.30	0.20	0.10	0.00
Survival probability	0.002	0.08	0.40	0.81	0.98	1
Mean population	6.0	17.8	25.9	36.46	47.49	56.88
Standard deviation	0	9.82	15.21	14.17	13.34	10.07

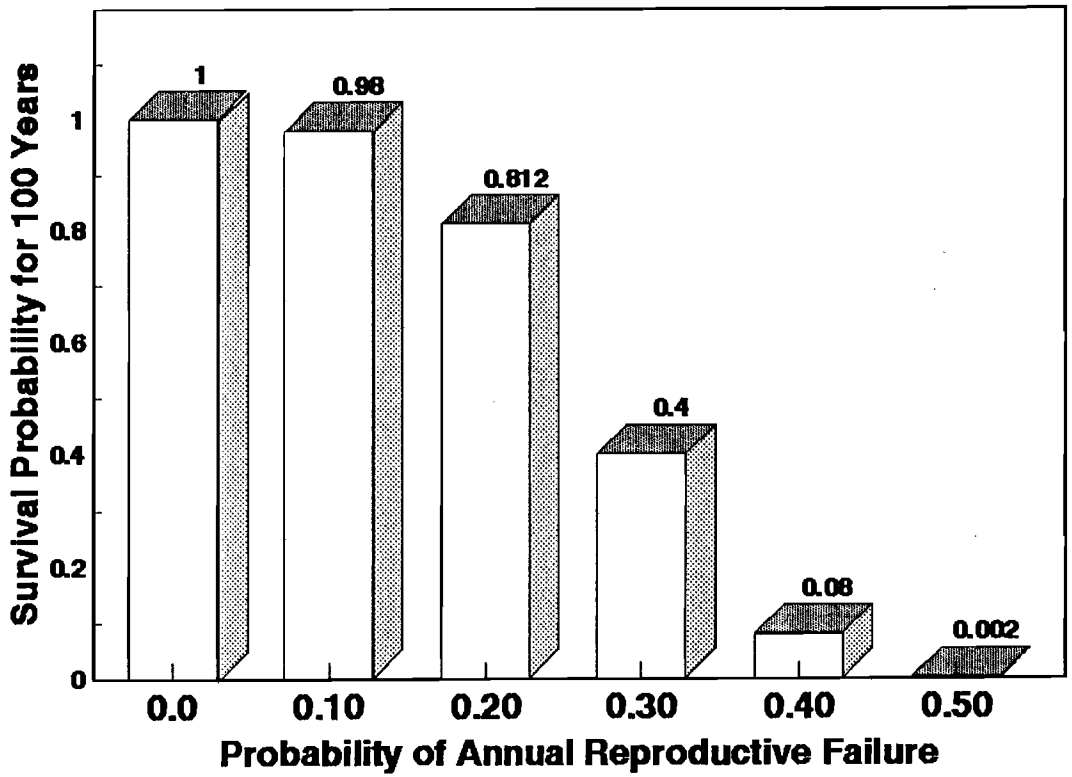
	Survival probabilities of adult Florida panthers used in above model runs												
Age class	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11	11-12	12-13	13-14
Females	.80	.90	.90	.90	.90	.90	.90	.90	.90	.80	.80	.80	.70
Males	.30	.40	.50	.60	.70	.80	.80	.80	.70	.70	.60	.60	.50

[1] Population size was limited to 70, kitten survival=0.80, probability=0.05, 0.20, 0.60, 0.10, 0.05 for litter sizes of 0, 1, 2, 3, 4, respectively, carrying capacity=60, standard deviation=10, subadult male survival dependent upon home range vacancies.

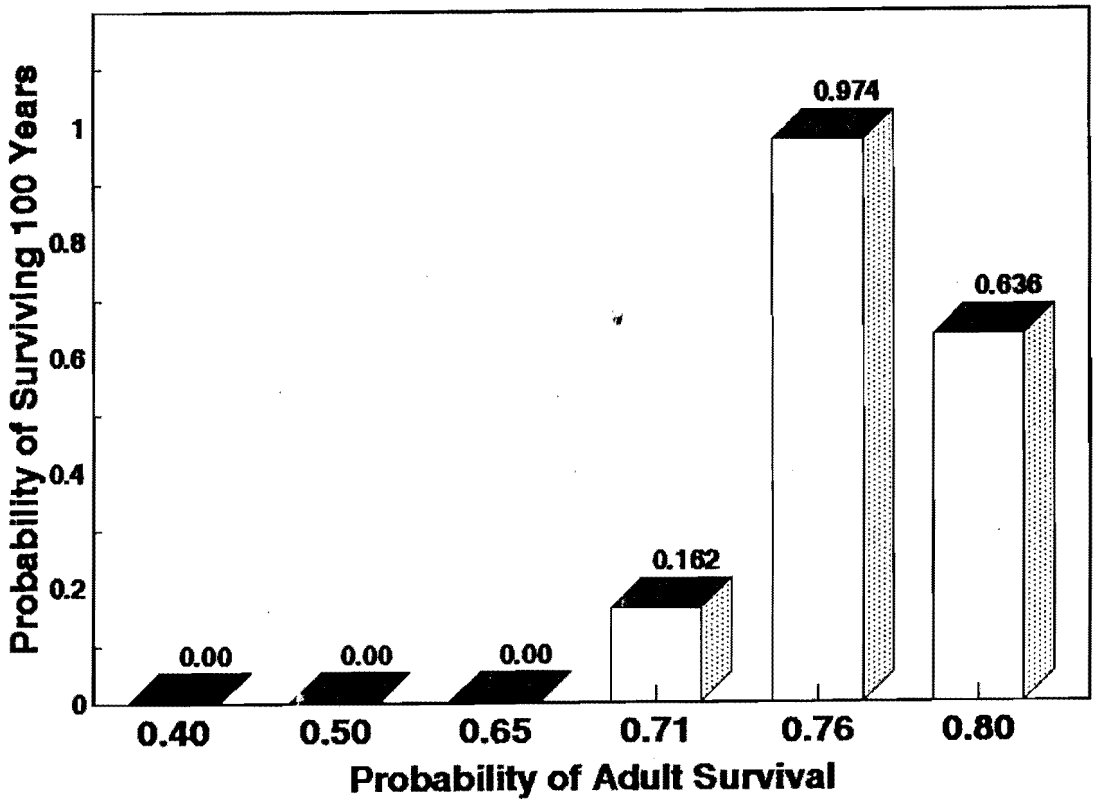
Table C-4. Effect of adult survival rates on Florida panther population persistence for 100 years[1].

Run	1		2		3		4	
Sex	F	M	F	M	F	M	F	M
Age class								
1-2	.7	.5	.7	.4	.8	.8	.8	.5
2-3	.7	.5	.8	.5	.8	.8	.9	.5
3-4	.8	.5	.9	.5	.8	.8	.9	.6
4-5	.8	.5	.9	.6	.8	.8	.9	.7
5-6	.8	.6	.9	.7	.8	.8	.9	.8
6-7	.8	.6	.9	.8	.8	.8	.9	.8
7-8	.8	.6	.9	.8	.8	.8	.9	.8
8-9	.8	.6	.8	.8	.8	.8	.9	.8
9-10	.8	.6	.8	.7	.8	.8	.8	.8
10-11	.7	.5	.7	.7	.8	.8	.8	.7
11-12	.7	.5	.7	.7	.8	.8	.8	.7
12-13	.7	.5	.6	.6	.8	.8	.7	.6
13-14	.7	.5	.6	.6	.8	.8	.7	.5
Mean survival rate	0.65		0.71		0.80		0.76	
Prob. of survival	0		0.162		.636		.974	
Mean population size	1.7		30.13		31.54		64.61	
Standard deviation	0		17.72		18.43		9.02	

[1] Population size was limited to 70, kitten survival=0.65, default litter sizes, no reproductive failures, no density dependent mechanisms.



C-3. Effect of reproductive failure on Florida panther population persistence for 100 years.



C-4. Effect of adult survival on Florida panther population persistence for 100 years.

rates in the wild population (Maehr 1991a, Maehr and Caddick 1995).

The popular citation of the Seal and Lacy (1989) simulation has reinforced an arguable interpretation of the panther's demographic status. Jordan (1993) underscored the need for reintroduction sites based on the VORTEX simulation's prediction of panther extinction within 25-40 years. Roelke and Glass (1992) listed a number of management actions that purportedly have been taken as the result of this model's prediction of a 6-10% population decline per year and a 3-7% annual loss of genetic diversity. Barrone et al. (1994) citing Roelke et al. (1993) conclude that the Florida panther population is not self sustaining because of high "infant" mortality and other factors described by Seal and Lacy (1989). As a result of the widespread citation of uncritically evaluated model results, the panther's dismal future has become a self-perpetuating truism.

Both the Abercrombie and VORTEX models predicted high probabilities of extinction when based on assumptions founded on mid-1980s field data or 'best guess' estimates. However, by increasing the survival probabilities of breeding females, and by increasing the survival of kittens to reflect field data, the outcomes of model runs change appreciably. Table C-5 contrasts several important parameter values and qualitative predictions that were incorporated in or deduced from the VORTEX and Abercrombie models. It is likely that an interaction of a smaller maximum population size, higher age of 1st female reproduction, and higher mortality estimates were responsible for the more pessimistic outcomes of the VORTEX simulations. Although genetic variability was not factored into Abercrombie's model and Seal and Lacy (1989:105) acknowledge that "we have no data on the effects of inbreeding on Florida panthers (or on any population of Felis concolor)," this aspect of natural history is likely of much less importance to this

Table C-5. Comparison of key parameter values for VORTEX and the Abercrombie model.

Parameter	Vortex[1]	Abercrombie
Maximum population	45	70[2]
Age of 1st female reproduction	3	2[3,4]
% of females with 0 young	50	18[4,a,b]
% mortality in 1st year	50	<20[4]
% annual adult mortality	25	17[5]
Overall mortality	High	Low[5]
Population demographics	Unstable	Stable[2]

[1] Based on best guess estimates
[2] Based on Maehr et al. 1991a
[3] Based on Maehr et al. 1989
[4] Based on current field data
[5] Based on Maehr et al. 1991b
[a] not used in Abercrombie model
[b] Mean successful birth interval for all female panthers (reproductively capable and incapable) is 23 months (n=17 inter-birth intervals including 2 females that did not reproduce over 37 and 44 month periods; range=14-44, successful range=14-38, successful mean =18.3)

small population's 20- to 50-year future than are normal demographics (Lande 1988, Caughley 1994, Caughley and Sinclair 1994:251) which panthers clearly exhibit (Maehr et al. 1991a, Maehr and Caddick 1995). Although O'Brien et al. (1990:492) used "reduced allozyme variation" as evidence of the panther "suffering from a history of inbreeding", there are no data to suggest the existence of any genetic differences between modern and pre-Columbian Florida panthers, nor have reported physical abnormalities such as deformed sperm or unusual pelage characteristics been linked to any demographic maladies. When one considers the geography of south Florida (i.e. its placement at the extremity of a peninsula), inbreeding has likely been commonplace for millennia. Further, because panther mortality rates are typical of unhunted western cougar populations (Maehr et al. 1991b), and very few resident breeding adults have died since 1986 (four males, three females), the claim of 3-7% annual loss of genetic diversity may be unrealistically high. While two to three panthers may die annually, these animals are mostly non-breeding males. Further, the assumption of high litter mortality is specious in light of very few documented deaths of kittens less than one year of age (Maehr and Caddick 1995). From 1986 through 1993, 10 radio-collared females produced a minimum of 48 kittens that were verified by observation. The fates of 32 of these kittens were documented. Ten were removed from the wild for captive breeding, four died (one cannibalized, one research accident, two hit by cars), and 18 survived to at least 12 months of age. If the kittens removed for captivity are ignored, panther kittens in southwest Florida exhibit an 82% survival rate. Another way of calculating kitten mortality is to compare the mean number of newborns with the mean number of litters

composed of older kittens. Based on six litters observed seven-14 days postpartum, the average number of kittens was 2.3 (range 1-3). Average litter size of kittens greater than four months of age was 2.0 (n=17, range 1-4). The difference between these means suggests a 13% kitten mortality rate. Mortality rates based on either method of calculation are low relative to other large cats. In addition, all three female panthers captured and radio-instrumented as kittens survived to establish home ranges and produce kittens of their own. In each case the female conceived her first litter by about 18 months of age (Maehr et al. 1989, Fla. Game and Fresh Water Fish Comm. unpub. data).

While the theory of small population genetics in vogue within some conservation biology circles predicts demographic collapse for the Florida panther, and some authors have suggested this already is underway, there are no data from the field to support this notion. The known demographics of the Florida panther suggest that the irreversible efforts to 'restore' the genetic make up of the population are currently unnecessary, and that conservation efforts should be directed toward the causes of small population size rather than symptoms of a small population.

APPENDIX D

THE FLORIDA PANTHER: ALL PRESENT AND ACCOUNTED FOR?

Before the advent of radio-telemetry studies, Highlands and Glades counties were considered the heart of the Florida panther's (Felis concolor coryi) modern range (Layne and McCauley 1976). More published accounts and other verified records of the panther came from this rural area during the period 1955-1975 than any other part of the state. Since 1975 records have continued to accumulate, and yet, there has been no persistent effort to determine the significance of these observations. The few excursions into south central Florida panther ecology have been sporadic, opportunistic, short-lived, and inconclusive (Nowak and McBride 1973, Roof and Maehr 1988, Maehr et al. 1992). With the human population in this area expected to increase by as much as 45% over the years 1990 to 2000 (Fernald and Purdum 1992:254), the current status of panthers may soon be forever a mystery.

Florida panther recovery has taken many twists and turns since the first panther in modern times was treed by Roy McBride in Glades County on 10 February 1973 (Nowak and McBride 1973). This animal, an old, decrepit female was the only living animal handled in this part of the panther's range for 15 years. In the interim, nearly two dozen

panthers were captured and radio-collared in Collier and Hendry counties where Florida natural resources agencies focused most of their panther research energies. As the result of repeated capture successes in the Big Cypress region, interest in searching for other Florida population centers waned. It seemed that the old Glades County female would forever be an enigma; no more than the last of her line in south central Florida.

Meanwhile, management strategies for this endangered subspecies changed from the experimental approach to captive breeding as outlined in the Florida panther recovery plan (U.S. Fish and Wildlife Service 1987), to an "emergency", accelerated removal program developed by the Captive Breeding Specialists Group (Seal and Lacy 1989), and most recently to a genetic restoration plan (Captive Breeding Specialist Group 1992) that has left the fate of a handful of captive panthers in doubt. None of these plans have included recommendations to search for additional panther populations outside of south Florida.

Nonetheless, as is characteristic of mountain lion populations throughout the Western Hemisphere, evidence of their occupation in south central Florida was hard to repress. Just as Florida's unique black bobcats periodically surface in south central Florida without anyone actively searching for them (Regan and Maehr 1990), so did panthers in Highlands County on 12 August 1987 with the discovery of tracks and scat at Archbold Biological Station (Layne and Wassmer 1988). Five months later, male panther #24 was captured and radio-instrumented like so many of his con(sub)specifics 100 km to the south (Maehr et al. 1992). While panther #24 opened a new door into Florida panther distribution and habitat use, he appeared to do little to confirm breeding in this disjunct area dominated by privately-owned cattle ranches (Maehr 1990). His mysterious death on

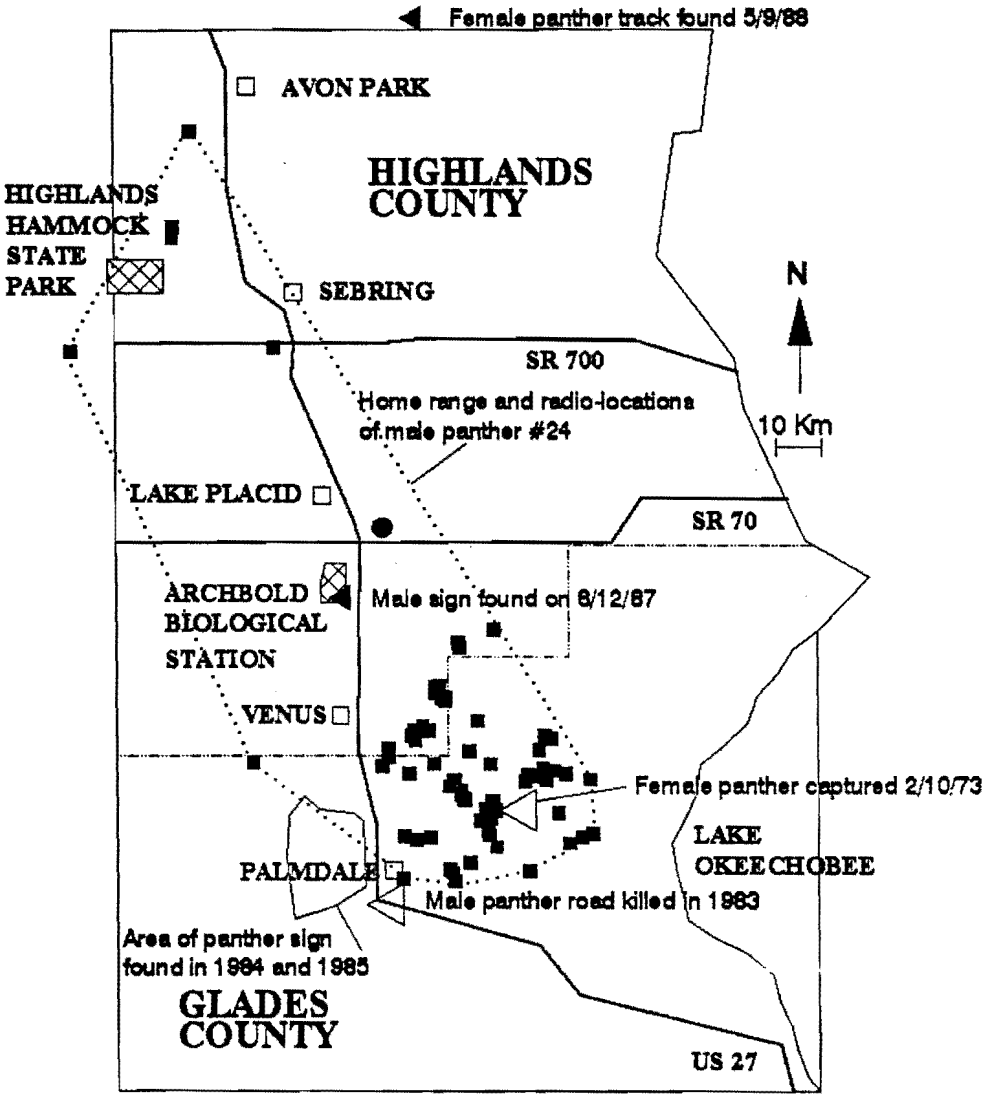


Figure D-1. Distribution of verified panther sign in and around Highlands County and Glades County, Florida from 1973 through 1988. Dotted line and solid squares represent male panther #24's home range and radio locations, respectively.

22 August 1988 shut this door which has remained unopened ever since. Although verified sign of at least one other panther turned up near Avon Park after #24's capture (Fig. D-1), searches for additional cats have been in limbo for nearly eight years.

The recent history of panthers in south central Florida is incomplete, and without more thorough investigations, their significance and relationship to the heavily-studied breeding core in southwest Florida is open to speculation. Number 24 possessed a crooked tail and an obvious dorsal cowlick; the classic phenotypic characteristics of most panthers in south Florida. On the other hand, telemetry data spanning 13 years have failed to document a demographic link between south central Florida and the Big Cypress Swamp, even though black bears have demonstrated this capability (Maehr et al. 1988). Two explanations seem capable of explaining what has been observed in the northern limits of the panther's known range in Florida. First, #24 may have been captured following an unprecedented one-way dispersal across the Caloosahatchee River from Hendry or Lee county. Finding no other panthers on the north side of the river, he was destined to a futile, solitary existence. His death, then, was of no consequence to the population. An alternative explanation is that the Caloosahatchee River may, indeed, be a barrier to panther movements. Although a natural land bridge once maintained a wide, dry connection between these now-disjunct areas, dredging and lengthening of this once-shallow channel have created a formidable obstacle to the travels of the uplands-preferring panther. If the latter scenario describes recent events, then a reasonable explanation for the appearance of #24 is that a breeding, resident population of Florida panthers exists north of the Caloosahatchee River.

The significance of a naturally-occurring second population of Florida panthers should be obvious even if one ignores the principal recovery goal to establish two additional "self-sustaining populations within the historic range of the animal" (U.S. Fish and Wildlife Service 1987:14). It would seem prudent that all efforts be made to scour Florida's hinterlands, especially in areas with recent, verified evidence of occupation, before large numbers of wild panthers are brought into captivity, and before the genetic character of the only known wild population is forever altered with the introduction of genes originating from over 1000 km away. Despite unsubstantiated statements to the contrary (Barrone et al. 1994, Roelke and Glass 1992, Roelke et al. 1993), the south Florida panther population exhibits normal demographics, high female fertility, and frequent reproduction with high juvenile survival (Maehr et al. 1989, 1991a, 1991b, Maehr and Caddick 1995), and suggests that extreme genetic conservation measures are, as yet, unnecessary. The verification and study of individuals that may very well make up this second population should be of the highest priority for government agencies involved in panther recovery. Not only would a second, natural population increase the options for genetic management and decrease the likelihood that chance events could impact a single population, but it would significantly reduce the cost to taxpayers that would otherwise result from more symptom-oriented panther recovery. The cost of a multi-year, adequately-staffed search effort would be a wise investment, especially in light of the potential dividend. And, demographic analyses and positive trends in reproduction suggest that ample time exists before last-ditch, irreversible actions (that are moving forward now) are necessary.

While cougars are increasingly the subject of intensive searches throughout their former range in eastern North America (i.e. McBride et al. 1993), where there is little unequivocal data to support the notion that they breed there, there is absolutely no effort being made in Florida to document the status of an area that has produced compelling artifacts of a population's existence. This evidence includes the two panthers captured in 1973 and 1988, a Glades County road kill in 1983 (U.S. 27 near Palmdale), and an adult male tracked by his sign for 12 months during 1984 and 1985 (Roof and Maehr 1988)(Fig. D-1). Several other reports from nearby Highlands County were detailed by Layne and Wassmer (1988). When considered from a regional perspective, the Glades and Highlands county records appear to form an even larger complex of records extending up the St. Johns River basin. Even for the skeptic, it should be difficult to ignore the possibility of a second wild population of Florida panthers in south central Florida. It is ironic that the U.S. Fish and Wildlife Service in conjunction with the Arkansas Game and Fish Commission and the U.S. Forest Service recently funded a three-year survey for panthers in Arkansas (McBride et al. 1993). Even though this very extensive effort failed to uncover evidence of a population in the remote regions of this wild state, it proved that government agencies can unite to pursue the difficult task of searching for the phantom cat of the East.

Some could argue that the failure to find cougars or their sign has the potential to shred the fabric of local folklore in places where the myth of large cats (tawny, black, spotted, or otherwise) is more important than any alternate and provable reality. On the other hand, discovery and documentation opens a Pandora's box of agency management

options, none of which are particularly inexpensive, easy, nor welcome. Managing populations of cougars requires nearly unlimited space that often is privately-owned and used for purposes that can be incompatible with large, solitary, wide-ranging felids. There is little doubt that for panther recovery to proceed in south central Florida, creative approaches much be applied. All too often, the treatment of symptoms characteristic of small populations and populations living at distributional extremes have outweighed decisions to address the root of the panther's problems: dwindling space. In the meantime, thousands of square kilometers and an untold number of Florida panthers remain present and unaccounted for.

APPENDIX E

VITAL STATISTICS OF SOUTH FLORIDA PANTHERS, 1981--1993

Table E-1. Florida panthers captured in the wild in south Florida from 1981 to 1994. Causes of death are HBC=Hit by car, IA=Intraspecific aggression, Drug OD=Drug overdose, Heart fail=Congestive heart failure, P. rabies=Pseudorabies, Puncture=Esophageal puncture, ?=unknown. Total radio locations= 31,936.

ID #	Sex	Mass (kg) at first capture	Age at 1st capture (years)	Date of capture	Date of death[1]	Cause of death	Number of radio locations
01	M	54.4	10	2/10/81	12/14/83	HBC	47
02	M	49.0	10	2/20/81	11/29/84	IA	473
03	F	30.8	9	1/23/82	1/17/83	OD	192
04	M	51.2	8	1/27/82	4/18/85	HBC	325
05	F	44.7	8	2/23/82	11/23/82	?	307
06	M	55.3	7	2/27/82	4/16/82	?	0
07	M	55.3	6	3/2/82	10/26/85	HBC	231
08[3]	F	33.9	7	3/25/84	8/20/88	old age	245
09	F	35.8	3	1/26/85	-		1426
10	M	15.4	0.4	1/15/86	1/27/87	IA	207
11	F	41.7	4	1/21/86	-		1412
12	M	55.3	5	1/28/86	11/9/94	IA	1406
13	M	57.1	4	2/27/86	12/14/87	HBC	313
14	F	32.2	5	12/7/86	6/20/91	?	1282
15	F	32.6	5	12/13/86	6/10/88	IA	505
16	M	39.0	1	1/12/87	-		1920
17	M	64.4	7	1/20/87	7/20/90	?	554
18	F	45.3	8	1/22/87	10/1/90	IA	595
19	F	22.2	0.7	2/9/87	-		1200
20	M	67.1	3	3/10/87	8/24/88	Heart fail	215
21[3]	F	25.4	1	3/16/87	-		469
22	F	14.7	0.5	3/18/87	7/22/91	Infection	700
23	F	14.1	0.5	3/18/87	-		1492
24	M	57.1	3	1/30/88	8/28/88	?	59
25	M	54.9	4	2/16/88	8/26/88	IA	87
26	M	54.4	5	3/1/88	7/8/94	IA	954

Table E-1. (continued)

ID #	Sex	Mass (kg) at first capture	Age at 1st capture (years)	Date of capture	Date of death	Cause of death	Number of radio locations
27	F	22.7	2	4/11/88	7/23/89	?	451
28	M	47.6	1.5	11/29/88	9/25/92	IA	532
29	M	20.2	0.5	1/3/89	5/27/92	P.rabies	522
30	M	22.4	0.7	1/6/89	1/29/90	IA	203
31	F	38.5	8	1/12/89	3/3/94	HBC	805
32	F	32.2	2	2/3/89	-		906
33	M	41.7	1.5	3/5/89	11/25/89	Rabies	256
34	M	28.1	0.8	1/8/90	11/15/93	Puncture	576
35	M	23.6	0.8	1/15/90	1/24/90	Infection	0
36	F	49.0	5	1/27/90	-		723
37	M	46.3	4	1/30/90	11/26/90	HBC	128
38	F	44.4	4	2/8/90	8/4/94	Infection	927
39	M	46.3	3	2/19/90	6/18/90	Infection	81
40	F	29.5	2	2/26/90	-		585
41	F	27.7	2	2/28/90	9/21/90	IA	89
42	M	27.2	0.9	3/6/90	-		766
43	M	24.5	0.8	5/1/90	11/1/91	IA	222
44	M	15.0	0.5	4/30/91	7/6/93	IA	272
45	M	16.8	0.5	5/8/91	-		482
46	M	52.6	2	1/30/92	-		419
47	M	19.0	0.5	2/21/92	2/19/93	IA	150
48	F	11.3	0.3	2/24/92	-		416
49	F	32.2	2	2/25/92	?		78
50	M	28.1	0.6	3/4/92	12/6/93	HBC	256
51	M	49.0	3	3/26/92	-		407
52	F	17.7	0.5	5/5/92	1/14/95	HBC	387
53	M	27.2	0.8	2/10/93	2/26/93	IA	7
54	M	29.9	0.8	2/10/93	-		275
K1[2]	M	1.2	0.05	4/7/92	-		-
K2[2]	M	1.1	0.05	4/7/92	-		-
K3[2]	M	1.8	0.06	6/18/93	-		-
K4[2]	F	1.8	0.06	6/18/93	-		-
K5[2]	F	1.7	0.06	6/18/93	-		-
K6[2]	M	0.6	0.02	10/30/93	-		-
K7[2]	F	0.6	0.02	10/30/93	-		-
K8[2]	F	0.6	0.02	10/30/93	-		-
201[3]	M	15.4	0.6	2/20/91			-
202[3]	M	21.3	0.7	2/22/91			-
203[3]	M	20.4	0.7	2/25/91			-
204[3]	F	16.8	0.6	2/27/91			-
205[3]	F	14.3	0.5	5/3/91			-
206[3]	F	15.0	0.5	5/6/91			-
207[3]	M	26.8	0.7	3/4/92			-
208[3]	F	0.6	0.02	6/6/92			-

Table E-1. (continued)

ID #	Sex	Mass (kg) at first capture	Age at 1st capture (years)	Date of capture	Date of death	Cause of death	Number of radio locations
209[3]	F	0.8	0.02	8/20/92			-
210[3]	M	0.8	0.02	8/20/92			-

[1]No entry for date of death is the result of the study animal remaining alive, transmitter failure, or the study animal was not instrumented (i.e. neonate kittens and kittens removed for captive breeding).

[2]Neonates handled at natal dens.

[3]Removed from wild.

APPENDIX F

VITAL STATISTICS OF SOUTH FLORIDA BLACK BEARS, 1986--1993

Table F-1. Black bears captured in south Florida from 1986 to 1993. Causes of death are HBC=Hit by car, IA=Intraspecific aggression, ?=unknown. Total locations = 6,452.

ID #	Sex	Mass (kg) at first capture	Age at 1st capture (years)	Date of capture	Date of death[1]	Cause of death	Number of radio locations
F01	F	79.3	4.5	8/22/88	-		44
F02	F	101.1	7.2	5/9/91	-		128
F03	F	70.3	6.5	8/15/91	-		203
F04	F	63.5	6.5	8/15/91	-		183
F05	F	58.1	3.5	9/20/91	-		217
F06	F	40.8	1.6	10/28/91	11/5/93	HBC	139
F07	F	88.4	9.6	10/29/91	-		176
F08	F	111.6	7.7	11/5/91	-		162
F09	F	77.1	3.7	11/8/91	-		189
F10	F	75.7	3.7	11/14/91	-		227
F11	F	63.5	3.2	5/12/92	-		70
F12	F	77.1	4.3	6/1/92	-		181
F13	F	81.6	4.3	6/17/92	-		156
F14	F	55.3	2.5	8/13/92	-		168
F15	F	68.0	2.6	10/25/92	-		154
F16	F	49.9	2.6	10/27/92	-		45
F17	F	90.7	6.7	11/25/92	-		147
F18	F	84.8	3.7	11/27/92	-		1
F19	F	88.4	6.8	12/16/92	-		143
F20	F	31.7	1.5	7/28/93	-		58
F21	F	70.3	6 (est.)[2]	12/12/93	-		69
M01	M	88.4	2.5	5/4/86	7/28/96	shot	71
M02	M	95.2	2.5	9/30/90	-		193
M03	M	147.4	3.0	2/18/91	4/25/92	HBC	121
M04	M	108.9	2.5	7/26/91	10/23/91	poached	28
M05	M	89.8	2.5	8/5/91	-		15
M06	M	138.3	14.5	8/8/91	-		91
M07	M	99.8	2.5	8/11/91	-		44
M08	M	104.3	5.5	8/14/91	-		216
M09	M	99.8	2.5	8/27/91	8/3/92	poached	71

Table F-1. (continued)

ID #	Sex	Mass (kg) at first capture	Age at 1st capture (years)	Date of capture	Date of death	Cause of death	Number of radio locations
M10	M	47.6	1.5	9/16/91	9/30/92	IA	90
M11	M	56.7	1.5	9/24/91	9/23/92	poached	87
M12	M	147.4	14.5	9/25/91	2/25/92	poached	40
M13	M	154.2	3.5	10/18/91	-		229
M14	M	64.4	1.5	10/27/91	-		66
M15	M	82.1	2.5	11/11/91	-		59
M16	M	59.0	1.8	12/2/91	-		74
M17	M	124.7	3.0	1/19/92	-		23
M18	M	220.0	12.0	1/30/92	12/17/93	?	139
M19	M	172.4	6.0	2/6/92	-		35
M20	M	112.0	9.0	2/7/92	-		161
M21	M	31.7	1.3	5/23/92	-		66
M22	M	18.1	0.7	10/20/91	-		41
M23	M	7.2	0.5	8/15/91	-		59
M24	M	163.3	4.3	6/12/92	-		82
M25	M	139.7	6.5	7/30/92	-		49
M26	M	79.4	6.5	9/4/92	-		37
M27	M	65.8	3.5	10/4/92	-		70
M28	M	97.5	3.5	10/8/92	-		84
M29	M	124.7	4.5	10/8/92	-		129
M30	M	107.9	2.5	10/12/92	-		96
M31	M	104.3	14.7	11/10/92	1/25/93	poached	17
M32	M	59.0	1.7	11/18/92	7/18/93	HBC	47
M33	M	73.5	1.8	12/11/92	-		33
M34	M	65.8	1.8	12/15/92	-		55
M35	M	113.4	4.3	5/23/93	-		108
M36	M	165.6	9.3	5/26/93	-		109
M37	M	182.3	6.3	5/31/93	-		18
M38	M	69.8	1.3	6/10/93	-		12
M39	M	147.4	12.5	7/28/93	-		97
M40	M	53.5	1.5	7/28/93	-		32
M41	M	104.3	5.4	7/31/93	-		35
M42	M	142.9	5.5	8/12/93	-		93
M43	M	81.6	2.5	8/31/93	-		55
M44	M	24.9	0.6	9/8/93	-		66
C1[3]	F	1.2	0.02	3/9/93	-		-
C2[3]	M	1.2	0.02	3/9/93	-		-
C3[3]	F	1.2	0.02	3/9/93	-		-
C4[3]	M	1.3	0.02	3/9/93	-		-
C5[3]	F	1.0	0.02	3/11/93	-		-

[1]No entry for date of death is the result of the study animal remaining alive through 1994, transmitter failure, or collar drop-off.

[2]Tooth not pulled because bear had broken jaw as the result of a collision with automobile.

[3]Neonates handled in den at 9-11 days of age.

LITERATURE CITED

Abrahamson, W.G., and D.C. Hartnett. 1990. Pine flatwoods and dry prairies. Pages 103-149 in R.L. Myers and J.J. Ewel, eds. Ecosystems of Florida. Univ. of Central Florida Press, Orlando, Florida.

Alberta Forestry, Lands, and Wildlife. 1992. Management plan for cougar in Alberta. Wildl. Manage. Planning Series No. 5. Edmonton, Alberta. 91pp.

Allen, R. 1950. Notes on the Florida panther, Felis concolor coryi Bangs. J. Mammal. 31:279-280.

Alt, G.L. 1980. Rate of growth and size of Pennsylvania black bears. Pennsylvania Game News 51(12):7-17.

Amstrup, S.C., and J. Beecham. 1976. Activity patterns of radio-collared black bears in Idaho. J. Wildl. Manage. 40:340-348.

Anderson, A.E. 1983. A critical review of literature on puma (Felis concolor). Spec. Rept. No. 54. Colorado Div. Wildl. Ft. Collins, Colorado. 91pp.

Anderson, A.E., D.C. Bowden, D.M. Kattner. 1992. The puma on Uncompahgre Plateau, Colorado. Tech. Publ. No. 40. Colorado Div. Wildl., Ft. Collins, Colorado. 116pp.

Anderson, E.M. 1987. A critical review and annotated bibliography of literature on the bobcat. Spec. Rept. No. 62. Colorado Div. Wildl. Ft. Collins, Colorado. 61pp.

Anderson, S.B. 1989. Three-legged black bear, Ursus americanus, survives four years. Canadian Field-Nat. 103:85-86.

Arnett, R.H., Jr. 1985. American insects. Van Nostrand Reinhold Co. New York, NY. 850pp.

Ashman, D., G.C. Christensen, M.L. Hess, G.K. Tsukamoto, and M.S. Wickersham. 1983. The mountain lion in Nevada. Nevada Fish and Game Dept. P.R. Proj. W-48-15 Final Rep. 75pp.

Ayres, L.A., L.S. Chow, and D.M. Graber. 1986. Black bear activity patterns and human induced modifications in Sequoia National Park. Internat. Conf. Bear Research and Manage. 6:151-154.

Bailey, T.N. 1972. Ecology of bobcats with special reference to social organization. Ph.D. Thesis, Univ. Idaho, Moscow. 82pp.

Bailey, T.N. 1974. Social organization in a bobcat population. J. Wildl. Manage. 38:435-446.

Bangs, O. 1898. The land mammals of peninsular Florida and the coast region of Georgia. Proc. Boston Soc. Nat. Hist. 28:157-235.

Barrone, M.A., M.E. Roelke, J. Howard, J.L. Brown, A.E. Anderson, and D.E. Wildt. 1994. Reproductive characteristics of male Florida panthers: comparative studies from Florida, Texas, Colorado, Latin America, and North American zoos. J. Mammal. 75:150-162.

Bass, O.L., and D.S. Maehr. 1991. Do recent panther deaths in Everglades National Park suggest an ephemeral population? Nat. Geogr. Research and Explor. 7:427.

Beale, D.M., and A.D. Smith. 1973. Mortality of pronghorn antelope fawns in western Utah. J. Wildl. Manage. 37:343-352.

Beck, T.D.I. 1991. Black bears of west-central Colorado. Tech. Publ. No. 39. Colorado Division of Wildl., Ft. Collins, Colorado. 86pp.

Beecham, J.J. 1983. Population characteristics of black bears in west central Idaho. J. Wildl. Manage. 47:405-412.

Beecham, J.J., D.G. Reynolds, and M.G. Hornocker. 1983. Black bear denning activities and den characteristics in west-central Idaho. International Conf. Bear Research and Manage. 4:79-86.

Beeman, L.E., and M.R. Pelton. 1980. Seasonal foods and feeding ecology of black bears in the Smoky Mountains. International Conf. Bear Research and Manage. 4:141-148.

Behrend, D.F., and R.W. Sage. 1974. Unusual feeding behavior by black bears. J. Wildl. Manage. 38:570.

Beier, P, and S. Loe. 1992. A checklist for evaluating impacts to wildlife movement corridors. Wildl. Soc. Bull. 20:434-440.

Bekoff, M. 1982. Coyote. Pages 447-459 in J.A. Chapman and G.A. Feldhammer eds. Wild Mammals of North America. The Johns Hopkins University Press. Baltimore, Maryland.

Belden, R.C., and D.J. Forrester. 1980. A specimen of Felis concolor coryi in Florida. J. Mammal. 61:160-161.

Belden, R.C., W.B. Frankenberger, R.T. McBride, and S.T. Schwikert. 1988. Panther habitat use in southern Florida. J. Wildl. Manage. 52:660-663.

Belden, R.C., and B.W. Hagedorn. 1993. Feasibility of translocating panthers into northern Florida. J. Wildl. Manage. 57:388-397.

Berg, W.E. 1979. Ecology of bobcats in northern Minnesota. Bobcat Research Conf. Proc., Nat. Wildl. Fed. Sci. Tech. Series 6:55-61.

Beringer, J.J., S.G. Seibert, and M.R. Pelton. 1990. Incidence of road crossing by black bears on Pisgah National Forest, North Carolina. Internat. Conf. Bear Research and Manage. 8:85-92.

Bertram, B.C.R. 1979. Serengeti predators and their social systems. Pages 221-248 in A.R.E. Sinclair and M. Norton-Griffiths, eds. Serengeti: dynamics of an ecosystem. The Univ. of Chicago Press, Chicago, Illinois.

Bonner, F.T. 1971. Chemical contents of southern hardwood fruits and seeds. U.S. Forest Service Research Note SO-136. 3pp.

Boyce, M.S. 1992. Population viability analysis. Annu. Rev. Ecol. Syst. 23:481-506.

Boyd, D., and B. O'Gara. 1985. Cougar predation on coyotes. Murrelet 66:17.

Brady, J.R., and H.W. Campell. 1983. Distribution of coyotes in Florida. Fla. Field Nat. 11:40-41.

Brady, J.R., and D.S. Maehr. 1982. A new method for dealing with apiary-raiding black bears. Proc. Annu. Conf. Southeast. Fish and Wildl. Agencies 36:571-577.

Brady, J.R., and D.S. Maehr. 1985. Distribution of black bears in Florida. Florida Field Nat. 13:1-7.

Brenneman, R.L., and S.M. Bates. 1984. Land-saving action. Island Press, Covelo, California. 249pp.

Brisbin, I.L., Jr., G.C. White, and P.B. Bush. 1986. PCB intake and the growth of waterfowl: multivariate analyses based on a reparameterized Richards sigmoid model. Growth 50:1-11.

Brown, R.C. 1988. Florida's fossils. Pineapple Press, Sarasota, Florida. 208pp.

Buie, D.E., T.T. Fendley, and H. McNab. 1979. Fall and winter home ranges of adult bobcats on the Savannah River Plant, South Carolina. Bobcat Res. Conf. Proc., Nat. Wildl. Fed. Sci. Tech. Ser. 6:42-46.

Bunnell, F.L., and D.E.N. Tait. 1981. Population dynamics of bears- implications. Pages 75-98 in C.W. Fowler and T.D. Smith, eds. Dynamics of large mammal populations. John Wiley and Sons, New York, New York.

Burns, L.A. 1984. Productivity and water relations in the Fakahatchee Strand of south Florida. Pages 318-333 in K.C. Ewel and H.T. Odum, eds. Cypress swamps. Univ. of Florida Press, Gainesville, Florida.

Burt, W.H. 1975. A field guide to the mammals. 3rd edition, Houghton Mifflin, Boston, Massachusetts.

Carbyn, L.N. 1982. Coyote population fluctuations and spatial distribution in relation to wolf territories in Riding Mountain National Park, Manitoba. Can. Field Nat. 96:176-183.

Captive Breeding Specialist Group. 1992. Genetic management strategies and population viability of the Florida panther. Report of a workshop. White Oak Conservation Center, Yulee, Florida. 27pp.

Carlock, D.M., R.H. Conley, J.M. Collins, P.E. Hale, K.G. Johnson, A.S. Johnson, and M.R. Pelton. 1983. The tri-state black bear study. Tennessee Wildl. Resources Agency, Knoxville, Tennessee. 286pp.

Carter, L.J. 1974. The Florida experience: land and water policy in a growth state. Johns Hopkins Univ. Press, Baltimore, Maryland.

Case, T.J., and M.E. Gilpin. 1974. Interference competition and niche theory. Proc. Nat. Acad. Sci. USA 71:3073-3077.

Caughley, G. 1994. Directions in conservation biology. J. Animal Ecol. 63:215-244.

Caughley, G., and A.R.E. Sinclair. 1994. Wildlife ecology and management. Blackwell Scientific Publications. Boston, Massachusetts. 334pp.

Chapman, J.A., and G.A. Feldhammer. 1982. Wild mammals of North America. Johns Hopkins Univ. Press, Baltimore, Maryland. 1147pp.

Chapman, J.A., J.G. Hockman, and W.R. Edwards. 1982. Cottontails. Pages 83-123 in J.A. Chapman and G.A. Feldhammer, eds. Wild mammals of North America. The Johns Hopkins Univ. Press, Baltimore, Maryland.

Chepko-Sade, B.D., W.M. Shields, J. Berger, Z.T. Halpin, W.T. Jones, L.L. Rogers, J.P. Rood, and A.T. Smith. 1987. The effects of dispersal and social structure on effective population size. Pages 287-321 in B.D. Chepko-Sade, and Z.T. Halpin, eds. Mammalian dispersal patterns: the effects of social structure on population genetics. Univ. of Chicago Press, Chicago, Illinois.

Chitty, H. 1950. Canadian Arctic wildlife enquiry, 1943-1949, with a summary of results since 1933. J. Animal Ecol. 19:180-193.

Clevenger, A.P., F.J. Purroy, and M.R. Pelton. 1990. Movement and activity patterns of a European brown bear in the Cantabrian Mountains, Spain. Internat. Conf. Bear Research and Manage. 8:205-211.

Collins, J.M. 1973. Some aspects of reproduction and age structures in the black bear in North Carolina. Proc. Annu. Conf. Southeast. Fish and Wildl. Agencies 27:163-170.

Conner, M.D. 1982. Determination of bobcat (Lynx rufus) and raccoon (Procyon lotor) population abundance by radioisotope marking. M.S. Thesis. Univ. of Florida, Gainesville, Florida. 55pp.

Conti, J.A., D.J. Forrester, and J.R. Brady. 1983. Helminths of black bears in Florida. Proc. Helminthol. Soc. Wash. 50:252-256.

Cox, J., R. Kautz, M. MacLaughlin, and T. Gilbert. 1994. Closing the gaps in Florida's wildlife habitat conservation system. Florida Game and Fresh Water Fish Commission, Tallahassee, Florida. 239pp.

Craighead, F.C. 1971. The trees of south Florida. Vol. 1. Univ. of Miami Press, Coral Gables, Florida. 212 pp.

Crowe, D.M. 1975. Aspects of aging, growth, and reproduction of bobcats from Wyoming. J. Mammal. 56:177-198.

Cummings, M.W. 1973. Rodents and drip irrigation. Proc. Drip Irrigation Seminar, Agric. Ext. Serv., San Diego, California. 4:25-30.

Darwin, C. 1871. The descent of man, and selection in relation to sex. First ed. J. Murray, London.

Davis, J.H., Jr. 1943. The natural features of southern Florida, especially the vegetation and the Everglades. Fla. Geol. Surv. Bull. No. 25. Tallahassee, Florida.

De Bellevue, E.B. 1976. Hendry County: an agricultural district in a wetland region. South Florida Study. Center for Wetlands, University of Florida, Gainesville, Florida.

Dekker, D. 1983. Denning and foraging habits of red foxes, Vulpes vulpes, and their interactions with coyotes, Canis latrans, in central Alberta, 1972-1981. Can. Field Nat. 97:303-306.

Diamond, J. 1992. The third chimpanzee. Harper Collins Publ., New York, New York. 407pp.

Dibello, F.J., S.M. Arthur, and W.B. Krohn. 1990. Food habits of sympatric coyotes, Canis latrans, red foxes, Vulpes vulpes, and bobcats, Lynx rufus, in Maine. Canadian Field-Nat. 104:403-408.

Dixon, K.R. 1982. Mountain lion (Felis concolor). Pages 711-727 in J.A. Chapman and G.A. Feldhammer, eds. Wild mammals of North America. The Johns Hopkins Univ. Press, Baltimore, Maryland.

Doan-Crider, D.L. 1995. Population characteristics and home range dynamics of the black bear in northern Coahuila, Mexico. M.S. Thesis. Texas A&M Univ.-Kingsville, Kingsville, Texas. 117pp.

Doan-Crider, D.L., and E.C. Hellgren. 1996. Population characteristics winter ecology of black bears in Coahuila, Mexico. J. Wildl. Manage. 60:398-407.

Duever, M.J., J.E. Carlson, J.F. Meeder, L.C. Duever, L.H. Gunderson, L.A. Riopelle, T.R. Alexander, R.L. Myers, and D.P. Spangler. 1986. The Big Cypress National Preserve. Research Report No. 8. Nat. Audubon Soc. New York, New York. 444pp.

Eagar, D.C., and S.K. Stafford. 1974. A bibliography of the black bear (Ursus americanus) in North America. East. Workshop Black Bear Manage. and Research 2:229-238.

Eagle, T.C., and M.R. Pelton. 1983. Seasonal nutrition of black bears in the Great Smoky Mountains National Park. Internat. Conf. Bear Research and Manage. 5:94-101.

Eisenberg, J.F. 1989. Mammals of the neotropics: the northern tropics. Vol. 1. Univ. of Chicago Press, Chicago, Illinois. 449 pp.

Eloff, F.C. 1973. Lion predation in the Kalahari Gemsbok National Park. J. S. Afr. Wildl. Manage. Assoc. 3:59-63.

Elowe, K.D. 1987. Factors affecting black bear reproductive success and cub survival in Massachusetts. Ph.D. Thesis, Univ. Massachusetts, Amherst. 71pp.

Elowe, K.D., and W.E. Dodge. 1989. Factors affecting black bear reproductive success and cub survival. J. Wildl. Manage. 53:962-968.

Elton, C. 1942. Voles, mice, and lemmings. Clarendon Press, Oxford, England.

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

Erickson, A.W. 1957. Techniques for live-trapping and handling black bears. Transactions N. Amer. Wildl. Conf. 22:520-543.

Erickson, A.W. 1964. An analysis of black bear kill statistics for Michigan. Pages 68-102 in The black bear in Michigan. Michigan State Univ., Agric. Exp. Station Research Bull. No. 4.

Erickson, A.W., J. Nellor, and G.A. Petrides. 1964. The black bear in Michigan. Michigan State Univ. Agric. Exp. Station Research Bull. No. 4. 102pp.

Erlinge, S. 1974. Distribution, territoriality, and numbers of the weasel Mustela nivalis in relation to prey abundance. Oikos 25:308-314.

Errington, P.L. 1957a. Of men and marshes. The Iowa State Univ. Press, Ames, Iowa. 150pp.

Errington, P.L. 1957b. Of population cycles and unknowns. Cold Spring Harbor Symposia on Quantitative Biology 22:287-300.

Eubanks, A.L. 1976. Movements and activity of the black bear in Great Smoky Mountains National Park. M.S. Thesis, Univ. of Tennessee, Knoxville, Tennessee. 83pp.

Ewel, J.J. 1990. Introduction. Pages 3-10 in R.L. Myers and J.J. Ewel, eds. Ecosystems of Florida. Univ. Central Florida Press, Orlando, Florida.

Ewel, J.J., D.S. Ojima, D.A. Karl, and W.F. DeBusk. 1982. Schinus in successional ecosystems of Everglades National Park. Report T-676. Nat. Park Service, Homestead, Florida. 141pp.

Ewer, R.F. 1968. Ethology of mammals. Elek Science, London, England.

Fendley, T.T., and I.L. Brisbin. 1977. Growth curve analyses: investigations of a new tool for studying the effects of stress upon wildlife populations. Proc. Internat. Congress Game Biol. 13:337-350.

Fernald, E.A., and E.D. Purdum. 1992. Atlas of Florida. Univ. Press of Florida, Gainesville, Florida. 280pp.

Fleming, T.H. 1992. How do fruit- and nectar-feeding birds and mammals track their food resources? Pages 355-391 in M.D. Hunter, T. Ohgushi, and P.W. Price, eds. Effects of resource distribution on animal-plant interactions. Academic Press, Inc., San Diego, California.

Forrester, D.J. 1992. Parasites and diseases of wild mammals in Florida. Univ. Press of Florida, Gainesville, Florida. 459pp.

Forrester, D.J., J.A. Conti, and R.C. Belden. 1985. Parasites of the Florida panther (Felis concolor coryi). Proc. Helminthol. Soc. Wash. 52:95-97.

Forrester, D.J., M.G. Spalding, and J.B. Wooding. 1993. Demodicosis in black bears (Ursus americanus) from Florida. J. Wildl. Diseases 29:136-138.

Foster, M.L. 1992. Effectiveness of wildlife crossings in reducing animal/auto collisions on Interstate 75, Big Cypress Swamp, Florida. M.S. thesis Univ. of Florida, Gainesville. 103pp.

Franzmann, A.W., C.C. Schwartz, and R.O. Peterson. 1980. Moose calf mortality on the Kenai Peninsula, Alaska. J. Wildl. Manage. 44:764-768.

Franzmann, A.W., and C.C. Schwartz. 1986. Black bear predation on moose calves in highly productive versus marginal moose habitats on the Kenai Peninsula, Alaska. Alces 22:139-153.

Fuller, T.D., and L.B. Keith. 1980. Summer ranges, cover-type use, and denning of black bears near Fort McMurray, Alberta. Canadian Field-Nat. 94:80-83.

Garner, N.P. Seasonal movements, habitat selection, and food habits of black bears (Ursus americanus) in Shenandoah National Park, Virginia. M.S. Thesis, Virginia Polytech. Inst. and State Univ. Blacksburg, Virginia. 104pp.

Garshelis, D.L., and M.R. Pelton. 1981. Movements of black bears in the Great Smoky Mountains National Park. J. Wildl. Manage. 45:912-925.

Geist, V. 1987. Bergmann's rule is invalid. Can. J. Zool. 65:1035-1038.

Glass, C.M., R.G. McLean, J.B. Katz, D.S. Maehr, C.B. Cropp, L.J. Kirk, A.J. McKeirnan, and J.F. Evermann. 1994. Isolation of pseudorabies (Aujeszky's Disease) virus from a Florida panther. J. Wildl. Diseases 30:180-184.

Greig-Smith, P. 1964. Quantitative plant ecology, 2nd edition. Butterworth's and Co., Ltd. London.

Greiner, E.C., M.E. Roelke, C.T. Atkinson, J.P. Dubey, and S.D. Wright. 1989. Sacrosystis spp. in muscles of free-ranging Florida panthers and cougars (Felis concolor). J. Wildl. Diseases 25:623-628.

Guenther, D.D. 1980. Home range, social organization, and movement patterns of the bobcat Lynx rufus, from spring to fall in south-central Florida. M.A. Thesis, Univ. South Florida, Tampa, Florida. 66pp.

Gunther, K.A. 1990. Visitor impact on grizzly bear activity in Pelican Valley, Yellowstone National Park. Internat. Conf. Bear Research and Manage. 8:73-78.

Hall, E.R. 1951. American weasels. Univ. of Kansas Publ., Mus. of Nat. Hist. 4:1-466.

Hall, H.T., and J.D. Newsom. 1976. Summer home ranges and movements of bobcats in bottomland hardwoods of southern Louisiana. Proc. Annu. Conf. Southeast. Fish and Wildl. Agencies. 30:427-436.

Hamilton, D.A. 1982. Ecology of the bobcat in Missouri. M.S. Thesis, Univ. Missouri, Columbia. 152pp.

Hamilton, R.J., and R.L. Marchinton. 1980. Denning and related activities of black bears in the coastal plain of North Carolina. Internat. Conf. Bear Research and Manage. 4:121-126.

Hamilton, W.J., Jr. 1941. Notes on some mammals of Lee County, Florida. Amer. Midl. Nat. 25:686-691.

Hamilton, W.J., Jr., and R.P. Hunter. 1939. Fall and winter food habits of Vermont bobcats. J. Wildl. Manage. 3:99-103.

Hanby, J.P., and J.D. Bygott. 1979. Population changes in lions and other predators. Pages 249-262 in A.R.E. Sinclair and M. Norton-Griffiths, eds. Serengeti: dynamics of an ecosystem. The Univ. of Chicago Press, Chicago, Illinois.

Hardy, D.M. 1974. Habitat requirements of the black bear in Dare County, North Carolina. M.S. Thesis, Virginia Polytech. Inst. and State Univ. Blacksburg, Virginia. 121pp.

Harlow, R.F. 1959. An evaluation of white-tailed deer habitat in Florida. Tech. Bull. 5. Florida Game and Fresh Water Fish Commission, Tallahassee, Florida. 64pp.

Harlow, R.F. 1961. Characteristics and status of Florida black bear. Trans. N. Amer. Wildl. Conf. 26:481-495.

Harlow, R.F. 1962a. Osteometric data for the Florida black bear. Quart. J. Florida Acad. Sci. 25:257-273.

Harlow, R.F. 1962b. Facts about Florida black bear. Florida Wildl. 15:12-17.

Harris, L.D. 1984. The fragmented forest. Univ. of Chicago Press, Chicago, Illinois. 211pp.

Harris, L.D. 1988. The nature of cumulative impacts on biotic diversity of wetland vertebrates. Environmental Manage. 12:675-693.

Harris, L.D. 1990. What does geology have to do with panther conservation? Nat. Geographic Research and Explor. 7:117-119.

Harris, L.D., and P. Gallagher. 1989. New initiatives for wildlife conservation, the need for movement corridors. Pages 11-36 in G. Mackintosh, ed. In defense of wildlife: preserving communities and corridors. Defenders of Wildlife, Washington, D.C.

Harris, L.D., and J.G. Gosselink. 1990. Cumulative impacts of bottomland hardwood forest conversion on hydrology, water quality, and terrestrial wildlife. Pages 259-322 in J.G. Gosselink, L.C. Lee, and T.A. Muir, eds. Ecological processes and cumulative impacts: illustrated by bottomland hardwood wetland ecosystems. Lewis Publ., Inc., Chelsea, Michigan.

Harris, L.D., and W. Cropper. in press. Between the devil and the deep blue sea: implications of climate change for Florida's flora and fauna. in R. Peters and T. Lovejoy, eds. Global warming and biological diversity. Yale Univ. Press, New Haven, Connecticut.

Harrison, D.J. 1992. Dispersal characteristics of juvenile coyotes in Maine. J. Wildl. Manage. 56:128-138.

Harrison, D.J., J.A. Bissonette, and J.A. Sherburne. 1989. Spatial relationships between coyotes and red foxes in eastern Maine. J. Wildl. Manage. 53:181-185.

Hawbecker, A.C. 1939. Coyotes prey on goats. J. Mammal. 20:371-372.

Hawthorne, D.W. 1980. Wildlife damage and control techniques. Pages 411-439 in S.D. Schemnitz ed. Wildlife management techniques manual. The Wildl. Soc., Inc. Bethesda, MD.

Hedrick, P.W. 1995. Gene flow and genetic restoration: the Florida panther as a case study. Conserv. Biol. 9:996-1007.

Hela, I. 1952. Remarks on the climate of southern Florida. Bull. Marine Sci. of Gulf and Caribbean 2:438-447.

Hellgren, E.C., and M.R. Vaughan. 1988. Seasonal food habits of black bears in Great Dismal Swamp, Virginia-North Carolina. Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies 42:295-305.

Hellgren, E.C., and M. R. Vaughan. 1989. Denning ecology of black bears in a southeastern wetland. J. Wildl. Manage. 53:347-353.

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

Henry, J.A., K.M. Portier, and J. Coyne. 1994. The climate and weather of Florida. Pineapple Press, Sarasota, Florida. 279 pp.

Herrero, S. 1978. A comparison of some features of the evolution, ecology, and behavior of black and grizzly/brown bears. Carnivore 1:7-17.

Hill, E.P., P.W. Sumner, and J.B. Wooding. 1987. Human influences on range expansion of coyotes in the southeast. Wildl. Soc. Bull. 15:521-524.

Holler, N.R. 1992. Choctawhatchee Beach Mouse. Pages 76-86 in S.R. Humphrey, ed. Rare and endangered biota of Florida, vol. 1 mammals. Univ. Press of Florida, Gainesville, Florida.

Hopkins, R.A. 1989. Ecology of the puma in the Diablo Range, California. Ph.D. Dissertation, Univ. of California at Berkley, Berkley, California. 262pp.

Horn, H.S. 1983. Some theories about dispersal. Pages 54-62 in I.R. Swingland and P.J. Greenwood, eds. The ecology of animal movements. Clarendon Press, Oxford.

Hunter, M.D., and P.W. Price. 1992. Natural variability in plants and animals. Pages 1-12 in M.D. Hunter, T. Ohgushi, and P.W. Price, eds. Effects of resource

distribution on animal-plant interactions. Academic Press, Inc., San Diego, California.

Hutchinson, G.E. 1957. Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology 22:415-427.

Jalkotzy, M., I. Ross, and J.R. Gunson. 1992. Management plan for cougars in Alberta. Alberta Forestry, Lands, and Wildlife, Edmonton, Alberta. 91pp.

Jarman, P.J., and A.R.E. Sinclair. 1979. Feeding strategy and the pattern of resource partitioning in ungulates. Pages 130-163 in A.R.E. Sinclair and N. Norton-Griffiths, eds. Serengeti:dynamics of an ecosystem. Univ. of Chicago Press, Chicago, Illinois.

Johnson, K.G., and M.R. Pelton. 1979. Denning behavior of black bears in the Great Smoky Mountains National Park. Proc. Southeast. Assoc. Fish and Wildl. Agencies 33:239-249.

Johnson, K.G., and M.R. Pelton. 1980. Environmental relationships and the denning period of black bears in Tennessee. J. Mammal. 61:653-660.

Johnson, K.G., G.B. Schaller, and H. Jinchu. 1988. Comparative behavior of red and giant pandas in the Wolong Reserve, China. J. Mammal. 69:552-564.

Johnson, M.K., R.C. Belden, and D.R. Aldred. 1984. Differentiating mountain lion and bobcat scats. J. Wildl. Manage. 48:239-244.

Jones, H.L., and J.M. Diamond. 1976. Short-time base studies on turnover in breeding bird populations on the California Channel Islands. Condor 78:526-549.

Jonkel, C.J., and I. McT. Cowan. 1971. The black bear in the spruce-fir forest. Wildl. Monogr. 27:1-57pp.

Jordan, D.B. 1993. Preliminary analysis of potential Florida panther reintroduction sites. U.S. Fish and Wildlife Service. Gainesville, Florida. 15 pp.

Kale, H.W., II, 1965. Ecology and bioenergetics of the long-billed marsh wren in Georgia salt marshes. Publ. Nuttal Ornithol. Club 5:1-142.

Kautz, R.S., D.T. Gilbert, and G.M. Mauldin. 1993. Vegetative cover in Florida based on 1985-1989 Landsat Thematic Mapper imagery. Florida Scientist 56:135-154.

Kellyhouse. D.G. 1977. Habitat utilization by black bears in northern California. Int. Conf. Bear Research and Manage. 4:221-227.

Klenner, W. 1987. Seasonal movements and home range utilization patterns of the black bear, Ursus americanus, in western Manitoba. Canadian Field-Nat. 101:558-568.

Knick, S.T., and T.N. Bailey. 1986. Long distance movements by two bobcats from southern Idaho. Amer. Midl. Nat. 116:222-223.

Knick, S.T. 1990. Ecology of bobcats relative to exploitation and a prey decline in southeastern Idaho. Wildl. Monogr. 108:1-42.

Koehler, G.M., and M.G. Hornocker. 1991. Seasonal resource use among mountain lions, bobcats, and coyotes. J. Mammal. 72:391-396.

Kolenosky, G.B., and S.M. Strathearn. 1987. Winter denning of black bears in east-central Ontario. International Conf. Bear Research and Manage. 7:305-316.

Konecny, M.J. 1989. Movement patterns and food habits of four sympatric carnivore species in Belize, Central America. Pages 243-264 in K.H. Redford and J.F. Eisenberg eds. Advances in neotropical mammalogy. Sandhill Crane Press, Inc. Gainesville, Florida.

Kruuk, H., and M. Turner. 1967. Comparative notes on predation by lion, leopard, cheetah, and wild dog in the Serengeti area, East Africa. Mammalia 31:1-27.

Laing, S.P., and F.G. Lindzey. 1993. Patterns of replacement of resident cougars in southern Utah. J. Mammal. 74:1056-1058.

Lamprey, H.F. 1963. Ecological separation of the large mammal species in the Tarangire game reserve, Tanganyika. East African Wildl. J. 1:63-92.

Land, E.D., D.S. Maehr, J.C. Roof, and J.W. McCown. 1993. Mortality patterns of female white-tailed deer in southwest Florida. Proc. Annu. Conf. Southeast. Fish and Wildl. Agencies 47:176-184.

Lande, R. 1988. Genetics and demography in biological conservation. Science 241:1455-1460.

Landers, J.L., R.J. Hamilton, A.S. Johnson, and R.L. Marchinton. 1979. Foods and habitat of black bears in southeastern North Carolina. J. Wildl. Manage. 43:143-153.

Layne, J.N., and M.N. McCauley. 1976. Biological overview of the Florida panther. Pages 5-45 in P.C.H. Pritchard, editor. Proc. of the Florida panther conference. Florida Audubon Soc., Casselberry, Florida.

Layne, J.N., and D.A. Wassmer. 1988. Records of the panther in Highlands County, Florida. Florida Field Nat. 16:70-72.

Leberg, P.L., I.L. Brisbin, Jr., M.H. Smith, and G.C. White. 1989. Factors affecting the analysis of growth patterns of large mammals. J. Mammal. 70:275-283.

LeCount, A.L. 1983. Denning ecology of black bears in central Arizona. International Conf. Bear Research and Manage. 4:71-78.

LeCount. A.L. 1986. Black bear field guide. Spec. Rep. No. 16. Arizona Game and Fish Dept., Phoenix, Arizona. 130pp.

Lehner, P.N. 1976. Coyote behavior: implications for management. Wildl. Soc. Bull. 4:120-126.

Leighty, R.G., M.B. Marco, G.A. Swenson, R.E. Caldwell, J.R. Henderson, O.C. Olson, and G.C. Wilson. 1954. Soil survey of Collier County, Florida. Florida Agric. Exp. Stat. Univ. of Florida, Gainesville. 72pp.

Lembeck, M., and G.I. Gould, Jr., 1979. Dynamics of harvested and unharvested bobcat populations in California. Nat. Wildl. Fed. Sci. Tech. Ser. 6:53-54.

Lindzey, F.G., and E.C. Meslow. 1976a. Characteristics of black bear dens on Long Island, Washington. Northwest Sci. 50:236-242.

Lindzey, F.G., and E.C. Meslow. 1976b. Winter dormancy in black bears in southwestern Washington. J. Wildl. Manage. 40:408-415.

Lindzey, F.G., and E.C. Meslow. 1977a. Home range and habitat use by black bears in southwestern Washington. J. Wildl. Manage. 41:413-425.

Lindzey, F.G., and E.C. Meslow. 1977b. Population Characteristics of black bears on an island in Washington. J. Wildl. Manage. 41:408-412.

Litvaitis, J.A. 1992. Niche relations between coyotes and sympatric carnivora. Pages 73-85 in A.H. Boer, ed. Ecology and management of the eastern coyote. Wildl. Research Unit, Univ. of New Brunswick, Fredericton, New Brunswick.

Litvaitis, J.A., and D.J. Harrison. 1989. Bobcat-coyote niche relationship during a period of coyote population increase. Canadian J. Zool. 67:1180-1188.

Lockie, J.D. 1966. Territory in small carnivores. Symp. Zool. Soc. London 18:143-165.

Logan, K.A., and L.L. Irwin. 1985. Mountain lion habitats in the Big Horn Mountains, Wyoming. Wildl. Soc. Bull. 13:257-262.

Logan, K.A., L.L. Irwin, and R.R. Skinner. 1986. Characteristics of a hunted mountain lion population in Wyoming. J. Wildl. Manage. 50:648-654.

Logan, K.A., L.L. Sweanor, J.F. Smith, B.R. Spreadbury, and M.G. Hornocker. 1990. Ecology of an unexploited mountain lion population in a desert environment. Annual Report. Wildlife Research Inst. Moscow, Idaho. 130pp.

Loope, L.L., and N.H. Urban. 1980. A survey of fire history and impact in tropical hardwood hammocks in the east Everglades and adjacent portions of Everglades National Park. Report T-592. Nat. Park Service, Homestead, Florida. 48pp.

Loope, L.L., and V.L. Dunevitz. 1981. Investigations of early plant succession on abandoned farmland in Everglades National Park. Everglades Nat. Park South Florida Research Center Rep. No. T-644.

MacArthur, R.H., and R. Levins. 1967. The limiting similarity, convergence and divergence of coexisting species. Amer. Nat. 101:377-385.

Mack, J.A. 1990. Black bear dens in the Beartooth Face, south-central Montana. Internat. Conf. Bear Research and Manage. 8:273-278.

Maehr, D.S. 1982. Beekeeping enters the solar age. Amer. Bee J. 122:372-375.

Maehr, D.S. 1984. The black bear as a seed disperser in Florida. Florida Field Nat. 12:40-42.

Maehr, D.S. 1990. The Florida panther and private lands. Conserv. Biol. 4:167-170.

Maehr, D.S. 1992. Florida panther. Pages 176-189 in S.R.Humphrey, ed. Rare and endangered biota of Florida. Vol. 1. Mammals. Univ. Press of Florida, Gainesville, Florida.

Maehr, D.S. 1994. The Florida panther: all present and accounted for? In J. Tischendorf, ed. The Eastern Cougar Conference. In press.

Maehr, D.S., and J.R. Brady. 1982a. Florida black bear-beekeeper conflict: 1981 beekeeper survey. Amer. Bee J. 122:372-375.

Maehr, D.S., and J.R. Brady. 1982b. Fall food habits of black bears in Baker and Columbia counties, Florida. Proc. Annu. Conf. Southeast. Fish and Wildl. Agencies 36:565-570.

Maehr, D.S., and J.R. Brady. 1984a. Food habits of Florida black bears. J. Wildl. Manage. 48:230-235.

Maehr, D.S., and J.R. Brady. 1984b. Comparison of food habits in two north Florida black bear populations. Florida Sci. 47:171-175.

Maehr, D.S., and J.T. DeFazio. 1985. Foods of black bears in Florida. Florida Field Nat. 13:8-12.

Maehr, D.S., and J.R. Brady. 1986. Food habits of bobcats in Florida. J. Mammal. 67:133-138.

Maehr, D.S., J.N. Layne, E.D. Land, J.W. McCown, and J. Roof. 1988. Long distance movements of a Florida black bear. Fla. Field Nat. 16:1-6.

Maehr, D.S., E.D. Land, J.C. Roof, and J.W. McCown. 1989a. Early maternal behavior in the Florida panther (Felis concolor coryi). Amer. Midl. Nat. 122:34-43.

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

Maehr, D.S., J.C. Roof, E.D. Land, J.W. McCown, R.C. Belden, and W.B. Frankenberger. 1989c. Fates of wild hogs released into occupied Florida panther home ranges. Florida Field Nat. 17:42-43.

Maehr, D.S., R.C. Belden, E.D. Land, and L. Wilkins. 1990a. Food habits of panthers in southwest Florida. J. Wildl. Manage. 54:420-423.

Maehr, D.S., E.D. Land, J.C. Roof, and J.W. McCown. 1990b. Day beds, natal dens, and activity of Florida panthers. Proc. Annu. Conf. Southeast. Fish and Wildl. Agencies 44:310-318.

Maehr, D.S., E.D. Land, and J.C. Roof. 1991a. Social ecology of Florida panthers. Nat. Geogr. Research and Explor. 7:414-431.

Maehr, D.S., E.D. Land, and M.E. Roelke. 1991b. Mortality patterns of panthers in southwest Florida. Proc. Annu. Conf. Southeast Fish and Wildl. Agencies 45:201-207.

Maehr, D.S., and C.T. Moore. 1992. Models of mass growth for 3 North American cougar populations. J. Wildl. Manage. 56:700-707.

Maehr, D.S., and J.B. Wooding. 1992. Florida black bear. Pages 265-275 in S.R.Humphery, ed. Rare and endangered biota of Florida. Vol. 1. Mammals. Univ. Press of Florida, Gainesville, Florida.

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

Maehr, D.S., and G.B. Caddick. 1995. Demographics and genetic introgression in the Florida panther. Conserv. Biol. 9:1295-1298.

Maehr, D.S., and J.A. Cox. 1995. Landscape features and panthers in Florida. Conserv. Biol. 9:1008-1019.

Maehr, D.S., E.C. Greiner, J.E. Lanier, and D. Murphy. 1995. Notoedric mange in the Florida panther (Felis concolor coryi). J. Wildl. Diseases 31:251-254.

Major, J.T., and J.A. Sherburne. 1987. Interspecific relationships of coyotes, bobcats, and red foxes in western Maine. J. Wildl. Manage. 51:606-616.

Martin, A.C., and W.D. Barkley. 1961. Seed identification manual. Univ. of California Press. Berkeley, California. 221pp.

Matthews, N.E., and W.F. Porter. 1988. Black bear predation of white-tailed deer neonates in central Adirondacks. Canadian J. Zool. 66:1241-1242.

Mattson, D.J., R.R. Knight, and B.M. Blanchard. 1992. Cannibalism and predation on black bears by grizzly bears in the Yellowstone ecosystem, 1975-1990. J. Mammal. 73:422-425.

Mayr, E. 1976. Evolution and the diversity of life. The Belknap Press of Harvard University Press, Cambridge, Massachusetts.

McArthur, R.H. 1972. Geographical ecology. Princeton Univ. Press, Princeton, New Jersey. 269 pp.

McBride, R.T., R.M. McBride, J.L. Cashman, and D.S. Maehr. 1993. Do mountain lions exist in Arkansas? Proc. of the Annu. Conf. of Southeast. Fish and Wildl. Agencies 47:394-402.

McCord, C.M., and J.E. Cardoza. Bobcat and Lynx. Pages 728-768 in J.A. Chapman and G.A. Feldhammer, eds. Wild mammals of North America. The Johns Hopkins Univ. Press, Baltimore, Maryland.

McCown, J.W., D.S. Maehr, and J. Roboski. 1990. A portable cushion as a wildlife capture aid. Wildl. Soc. Bull. 18:34-36.

McCown, J.W., M.E. Roelke, D.J. Forrester, C.T. Moore, and J.C. Roboski. 1991. Physiological evaluation of two white-tailed deer herds in southern Florida. Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies 45:81-90.

McCullogh, D.R., and D.E. Ullrey. 1983. Proximate mineral and gross energy composition of white-tailed deer. J. Wildl. Manage. 47:430-441.

McIvor, D.E., J.A. Bissonette, and G.S. Drew. 1995. Taxonomic and conservation status of the Yuma mountain lion. Conserv. Biol. 9:1033-1040.

McLaughlin, G.S., M. Orstbaum, D.J. Forrester, M.E. Roelke, and J.R. Brady. 1993. Hookworms of bobcats (Felis rufus) from Florida. J. Helminthol. Soc. Wash. 60:10-13.

McLean, P.K. 1991. The demographic and morphological characteristics of black bears in the Smoky Mountains. Ph.D. Thesis, Univ. Tennessee, Knoxville, Tennessee. 206pp.

McPherson, B.F. 1984. The Big Cypress Swamp. Pages 69-78 in P.J. Gleason, ed. Environments of south Florida present and past II. Miami Geol. Soc., Coral Gables, Florida.

Mech, L.D. 1983. Handbook of animal radio-tracking. Univ. of Minnesota Press, Minneapolis, Minnesota. 107pp.

Meffe, G.K., and C.R. Carroll. 1994. Principles of conservation biology. Sinauer Associates, Inc. Sunderland, Massachusetts. 600 pp.

Mehrer, C.F. 1975. Some aspects of reproduction in captive mountain lions Felis concolor, bobcat Lynx rufus, and lynx Lynx canadensis. Ph.D. Diss., Univ. N. Dakota, Grand Forks, North Dakota. 155pp.

Merriam, G. 1995. Movement in spatially divided populations: responses to landscape structure. Pages 64-77 in W.Z. Lidicker, Jr., ed. Landscape approaches in mammalian ecology and conservation. Univ. of Minnesota Press, Minneapolis, Minnesota.

Miller, S.D., and D.W. Speake. 1979. Progress report: demography and home range of the bobcat in south Alabama. Nat. Wildl. Fed. Sci. Tech. Ser. 6:123-124.

Mills, M.G.L. 1984. Prey selection and feeding habits if the large carnivores in the southern Kalahari. Supplement to Koedoe 1984:281-294.

Mills, M.G.L., and M.E.J. Mills. 1982. Factors affecting the movement patterns of brown hyaenas, Hyaena brunnea, in the southern Kalahari. S. Afr. J. Wildl. Res. 12:111-117.

Moehlman, P.D. 1989. Intraspecific variation in canid social systems. Pages 143-163 in J.L. Gittleman ed. Carnivore behavior, ecology, and evolution. Cornell Univ. Press. Ithaca, New York.

Mohr, C.O. 1947. Table of equivalent populations of North American small mammals. Am. Midl. Nat. 37:223-249.

Mollohan, C.M. and A.L. Lecount. 1989. Problems of maintaining a viable black bear population in a fragmented forest. Conference on the Multiresource Management of Ponderosa Pine Forests, Northern Arizona University, November 1-16.

Murray, M.T. 1994. Saw palmetto: nature's answer to an enlarged prostate. Health Counselor 6(4):33-35.

Myers, N. 1977. The Cheetah's relationships to the spotted hyena: some implications for a threatened species. Pages 192-200 in R.L. Phillips and C. Jonkel eds. Proc. 1975 Predator Symp. Montana For. and Conserv. Exp. Stat., Univ. of Montana, Missoula, Montana.

Myers, R.L., and J.J. Ewel. 1990. Ecosystems of Florida. Univ. of Central Florida Press, Orlando, Florida. 765pp.

Mykytka, J.M., and M.R. Pelton. 1989. Evaluation of four standard home range methods based on movements of Florida black bear. Tenth Internat. Symp. Biotelemetry. Dep. Zool., Univ. of Arkansas, Fayettville, Arkansas.

Mykytka, J.M., and M.R. Pelton. 1990. Management strategies for Florida black bears based on home range habitat composition. Internat. Conf. Bear Research and Manage. 8:161-167.

National Wildlife Federation. 1977. Status of the bobcat, Lynx rufus. Appendix 1, in W.C. Brownlee, ed., Status of the bobcat (Lynx rufus) in Texas. Texas Parks and Wildl. Spec. Rept. Austin, Texas. 20pp.

Nellis, D.W. 1994. Seashore plants of south Florida and the Caribbean. Pineapple Press, Sarasota, Florida. 160pp.

Nelson, R.A., and T.D.I. Beck. 1984. Hibernation adaptation in the black bear: implications for management. Proc. East. Workshop Bear Manage. and Research 7:48-53.

Norton, P.M., and A.B. Lawson. 1985. Radio tracking of leopards and caracals in the Stellenbosch area, Cape Province. S. Afr. J. Wildl. Res. 15:17-24.

Nowak, R.M. 1991. Walker's mammals of the world. Vol. 1 and 2. Johns Hopkins Univ. Press, Baltimore, Maryland. 1629pp.

Nowak, R.M., and R.T. McBride. 1973. Feasibility of a study on the Florida panther. Report to the World Wildlife Fund. 13 pp mimeo.

Nowak, R.M., and R.T. McBride. 1974. Status of the Florida panther. Pages 232-235 in World Wildlife Yearbook, 1973-1974. World Wildl. Fund Morges, Switzerland.

O'Brien, S.J., D.E. Wildt, M. Bush, T.M. Caro, C. Fitzgibbon, I. Aggundy, R.E. Leakey. 1987. East African cheetahs: evidence for two population bottlenecks? Proc. Nat. Acad. of Sci. U.S.A. 84:508-511.

O'Brien, S.J., M.E. Roelke, N. Yuhki, K.W. Richards, W.E. Johnson, W.L. Franklin, A.E. Anderson, O.L. Bass, R.C. Belden, and J.S. Martenson. 1990. Genetic introgression within the Florida panther (Felis concolor coryi). Nat. Geogr. Research and Explor. 6:485-494.

Odum, W.E., and C.C. McIvor. 1990. Mangroves. Pages 517-548 in R.L. Myers and J.J. Ewel, eds. Ecosystems of Florida. Univ. Central Florida Press, Orlando, Florida.

Olmstead, I., and L.L. Loope. 1984. Plant communities of Everglades National Park. Pages 167-184 in P.J. Gleason, ed. Environments of south Florida present and past II. Miami Geol. Soc., Coral Gables, Florida.

Ozoga, J.J., and L.J. Verme. 1982. Predation by black bears on newborn white-tailed deer. J. Mammal. 63:695-696.

Paquet, P.C. 1991. Winter spatial relationships of wolves and coyotes in Riding Mountain National Park, Manitoba. J. Mammal. 72:397-401.

Paquet, P.C. 1992. Prey use strategies of sympatric wolves and coyotes in Riding Mountain National Park, Manitoba. J. Mammal. 73:337-343.

Parker, G. 1995. Eastern coyote: the story of its success. Nimbus Publ. Ltd., Halifax, Nova Scotia. 254 pp.

Pelton, M.R. 1982. Black bear. Pages 504-514 in J.A. Chapman and G.A. Feldhammer, eds. Wild mammals of North America. The Johns Hopkins Univ. Press, Baltimore, Maryland.

Pianka, E.R. 1986. Ecology and natural history of desert lizards. Princeton Univ. Press, Princeton, New Jersey.

Pirtle, E.C., M.E. Roelke, and J.R. Brady. 1986. Antibodies against pseudorabies virus in the serum of a Florida black bear cub. J. Am. Vet. Med. Assoc. 189:1164.

Pollack, E.M. 1951. Food habits of the bobcat in the New England states. J. Wildl. Manage. 15:209-213.

Powell, R.A. 1982. The fisher: life history, ecology, and behavior. Univ. Minnesota Press, Minneapolis, Minnesota. 217.

Progulske, D.R., Jr. 1982. Spatial distribution of bobcats and gray foxes in eastern Florida. M.S. Thesis, Univ. of Florida, Gainesville, Florida. 63pp.

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

Ramsey, M.A., and I. Stirling. 1984. Interactions of wolves and polar bears in northern Manitoba. J. Mammal. 65:693-694.

Rasmussen, D.I. 1941. Biotic communities of Kaibab Plateau, Arizona. Ecol. Monogr. 11:229-275.

Raybourne, J.W. 1976. A study of black bear populations in Virginia. Trans. Northeast. Section Wildl. Soc. 33:71-81.

Regan, T.W., and D.S. Maehr. 1990. Melanistic bobcats in Florida. Florida Field Nat. 18:84-87.

Reid, D., M. Jiang, Q. Teng, Z. Qin, and J. Hu. 1991. Ecology of the Asiatic black bear (Ursus thibetanus) in Sichuan, China. Mammalia 55:221-237.

Reynolds, D.G., and J.J. Beecham. 1980. Home range activities and reproduction of black bears in west-central Idaho. Internat. Conf. Bear Research and Manage. 4:181-190.

Richards, F.J. 1959. A flexible growth function for empirical use. J. Exp. Bot. 10:290-300.

Richards, P.W. 1952. The tropical rain forest. Cambridge Univ. Press, Cambridge, Great Britain. 450 pp.

Robbins, C.T. 1983. Wildlife feeding and nutrition. Academic Press. New York, New York. 343pp.

Robel, R.J., A.D. Dayton, F.R. Henderson, R.L. Meduna, and C.W. Spaeth. 1981. Relationships between husbandry methods and sheep losses to canine predators. J. Wildl. Manage. 45:894-911.

Robertson, W.B. 1955. An analysis of the breeding-bird populations of tropical Florida in relation to the vegetation. Ph.D. Diss. Univ. of Illinois, Urbana, Illinois. 599pp.

Robertson, W.B., Jr., and J.A. Kushlan. 1974. The southern Florida avifauna. Pages 414-452 in P.J. Gleason II, ed. Environments of south Florida: past and present. Memoir 2. Miami Geol. Soc.

Robinson, W.B. 1952. Some observations of coyote predation in Yellowstone National Park. J. Mammal. 33:470-476.

Robinson, W.B., and E.F. Grand. 1958. Comparative movements of bobcats and coyotes as disclosed by tagging. J. Wildl. Manage. 22:117-122.

Robson, M.S. 1992. Florida red wolf. Pages 29-34 in S.R.Humphery, ed. Rare and endangered biota of Florida. Vol. 1. Mammals. Univ. Press of Florida, Gainesville, Florida.

Roelke, M.E., E.R. Jacobson, G.V. Kollias, and D.J. Forrester. 1985. Medical management and biomedical findings on the Florida panther, Felis concolor coryi, July 1, 1985 to June 30, 1986. Annu. Rept. Florida Game and Fresh Water Fish Comm., Tallahassee, Florida. 65pp.

Roelke, M.E., and C. M. Glass. 1992. Pages 38-43 in R.E. Junge, ed. Strategies for the management of the endangered Florida panther (Felis concolor coryi) in an ever shrinking habitat. Proc. Joint Conf. Am. Assoc. Zoo Veterinarians and Amer. Assoc. Wildl. Veterinarians.

Roelke, M.E., J.S. Martenson, and S.J. O'Brien. 1993a. The consequences of demographic reduction and genetic depletion in the endangered Florida panther. Current Biology 3:340-350.

Roelke, M.E., D.J. Forrester, E.R. Jacobson, G.V. Kollias, F.W. Scott, M.C. Barr, J.F. Evermann, and E.C. Pirtle. 1993b. Seroprevalence of infectious disease agents in free-ranging Florida panthers (Felis concolor coryi). J. Wildl. Diseases 29:36-49.

Rogers, L.L. 1976. Effects of mast and berry crop failures on survival, growth, and reproductive success of black bears. Transactions N. Amer. Wildl. and Natural Resources Conf. 41:431-438.

Rogers, L.L. 1987a. Effects of food supply and kinship on social behavior, movements, and population growth of black bears in northeastern Minnesota. Wildl. Monogr. 97:1-72pp.

Rogers, L.L. 1987b. Factors influencing dispersal in the black bear. Pages 75-84 in B.D. Chepko-Sade, and Z.T. Halpin, eds. Mammalian dispersal patterns. Univ. of Chicago Press, Chicago, Illinois.

Rogers, L.L., and L.D. Mech. 1981. Interactions of wolves and black bears in northeastern Minnesota. J. Mammal. 62:434-436.

Rolley, R.E., and W.D. Warde. 1985. Bobcat habitat use in southeastern Oklahoma. J. Wildl. Manage. 49:913-920.

Roof, J.C., and D.S. Maehr. 1988. Sign surveys for panthers on peripheral areas of their known range. Florida Field Nat. 16:81-85.

Rosenzweig, M.L. 1966. Community structure in sympatric carnivora. J. Mammal. 47:602-612.

Rosenzweig, M.L. 1967. The strategy of body size in mammalian carnivores. Amer. Midl. Nat. 80:299-315.

Ross, P.I., G.E. Hornbeck, and B.L. Horejsi. 1988. Late denning black bears killed by grizzly bear. J. Mammal. 69:818-820.

Roth, H.U. 1983. Diel activity of a remnant population of European brown bears. Internat. Conf. Bear Research and Manage. 5:223-229.

Roth, H.U., and D. Huber. 1986. Diel activity of brown bears in Plitvice Lakes National Park, Yugoslavia. Internat. Conf. Bear Research and Manage. 6:177-181.

Ruff, R.L. 1978. A study of the natural regulatory mechanisms acting on an unhunted population of black bears near Cold Lake, Alberta. Dept. of Wildl. Ecology, University of Wisconsin, Madison, Wisconsin. 107pp.

Ryden, H. 1975. God's dog. Coward, McCann, and Geoghagen, Inc. New York, New York. 288pp.

Sampson, F.W., and A. Brohn. 1955. Missouri's program of extension predator control. J. Wildl. Manage. 19:272-280.

Sargeant, A.B., S.H. Allen, and J.O. Hastings. 1987. Spatial relations between sympatric coyotes and red foxes in North Dakota. J. Wildl. Manage. 51:285-293.

Sauer, P.R. 1975. Relationship of growth characteristics to sex and age for black bears from the Adirondack region of New York. New York Fish and Game J. 22:81-113.

Schaller, G.B. 1972. The Serengeti lion: a study of predator-prey relations. Univ. of Chicago Press, Chicago, Illinois. 480 pp.

Schaller, G.B., and P.G. Crawshaw, Jr. 1980. Movement patterns of jaguar. Biotropica 12:161-168.

Schaller, G.B., T. Qitao, K.G. Johnson, W. Xiaoming, S. Heming, and H. Jinchu. 1989. The feeding ecology of giant pandas and Asiatic black bears in the Tangjiahe Reserve, China. Pages 212-241 in J.L. Gittleman, ed. Carnivore behavior, ecology, and evolution. Cornell Univ. Press, Ithaca, New York.

Schemnitz, S.D. 1974. Populations of bear, panther, alligator and deer in the Florida Everglades. Florida Scientist 37:156-167.

Schoener, T.W. 1974. Resource partitioning in ecological communities. Science 185:27-39.

Schopmeyer, C.S. 1974. Seeds of woody plants in the United States. Agric. Handbook No. 450. U.S. Dept. Agriculture. Washington, D.C. 883pp.

Schortemeyer, J.L., D.S. Maehr, J.W. McCown, E.D. Land, and P.D. Manor. 1991. Prey management for the Florida panther: a unique role for managers. Trans. N. Amer. Wildl. Conf. 56:512-526.

Schwartz, C.C., S.D. Miller, and A.W. Franzmann. 1987. Denning ecology of three black bear populations in Alaska. Internat. Conf. Bear Research and Manage. 7:281-291.

Schwartz, C.C., and A.W. Franzmann. 1991. Interrelationship of black bears to moose and forest succession in the northern coniferous forest. Wildl. Monogr. 113:1-58.

Seal, U.S. (editor). 1992. Genetic management strategies and population viability of the Florida panther (Felis concolor coryi). Report of a workshop to the U.S. Fish and Wildlife Service. Captive Breeding Specialist Group, IUCN. Apple Valley, Minnesota.

Seal, U.S., and R. Lacy. 1989. Florida panther population viability analysis. Report to the U.S. Fish and Wildlife Service. Captive Breeding Specialist Group, IUCN. Apple Valley, Minnesota.

Seidensticker, J. 1976. On the ecological separation between tigers and leopards. Biotropica 8:225-234.

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

Selander, R.K. 1966. Sexual dimorphism and differential niche utilization in birds. Condor 68:113-151.

Shannon, C.E., and W. Weaver. 1963. The mathematical theory of communication. Univ. of Illinois Press. Urbana, Illinois.

Shelford, V.E. 1963. The ecology of North America. Univ. of Illinois Press, Urbana, Illinois. 610 pp.

Shields, W.M. 1987. Dispersal and mating systems: investigating their causal connections. Pages 3-24 in B.D. Chepko-Sade, and Z.T. Halpin, eds. Mammalian dispersal patterns: the effects of social structure on population genetics. Univ. of Chicago Press. Chicago, Illinois.

Short, H.L., R.M. Blair, and E.A. Epps. Composition and digestibility of deer browse in southern forests. U.S. Forest Service Research Paper. SO-111. 10pp.

Simberloff, D.S., J.A. Farr, J.Cox, and D.W. Mehlman. 1992. Movement corridors: conservation bargains or poor investments? Conserv. Biol. 6:493-504.

Smith, T.R. 1985a. Observations of a tufted titmouse and a cattle egret associating with a black bear. Wilson Bull. 97:395.

Smith, T.R. 1985b. Ecology of black bears in a bottomland hardwood forest in Arkansas. Ph.D. Diss. Univ. of Tennessee, Knoxville, Tennessee. 209pp.

Smith, T.R., and O.L. Bass. 1994. Landscape, white-tailed deer, and the distribution of Florida panthers in the Everglades. Pages 693-708 in S. Davis, and J. Ogden, eds. Everglades: the ecosystem and its restoration. St. Lucie Press, Delray Beach, Florida.

Snyder, J.R., A. Herndon, and W.B. Robertson, Jr. 1990. South Florida rockland. Pages 230-277 in R.L. Myers and J.J. Ewel, eds. Ecosystems of Florida. Univ. Central Florida Press, Orlando, Florida.

Soil Conservation Service. 1981. 26 ecological communities of Florida. U.S. Dept. of Agric. Fort Worth, Texas.

Stafford, S.K., and L.E. Williams, Jr. 1968. Data on capturing black bears with alpha-chloralose. Proc. Annu. Conf. Southeast. Fish and Wildl. Agencies 22:161-165.

Stelmock, J.J., and F.C. Dean. 1986. Brown bear activity and habitat use, Denali National Park-1980. Internat. Conf. Bear Research and Manage. 6:155-167.

Stevenson, G.B. 1974. Palms of south Florida. George B. Stevenson (distr. by Fairchild Tropical Garden), Miami, Florida. 251pp.

Stirling, I., and A.E. Derocher. 1989. Factors affecting the evolution and behavioral ecology of the modern bears. Internat. Conf. Bear Res. and Manage. 8:189-204.

Stone, W.B., D.E. Roscoe, and B.L. Weber. 1975. A black bear suffering from paralysis of the hindquarters. New York Fish and Game J. 22:159-160.

Storer, R.W. 1955. Weight, wing area, and skeletal proportions in three accipiters. Acta Cong. Intern. Ornithol. 11:278-290.

Stuwe, M. 1985. McPaal: micro-computer programs for the analysis of animal locations. Version 1.2. Smithsonian Inst., Washington, D.C.

Sunquist, F. 1987. Latin America. Pages 60-83 in Kingdom of cats. Nat. Wildl. Fed. Washington, D.C.

Sunquist, M.E., F. Sunquist, and D.E. Daneke. 1989. Ecological separation in a Venezuelan Llanos carnivore community. Pages 197-232 in K.H. Redford and J.F. Eisenberg, eds. Advances in neotropical mammalogy. Sandhill Crane Press, Gainesville, Florida.

Sweanor, L. L. 1990. Mountain lion social organization in a desert environment. M.S. Thesis, Univ. of Idaho, Moscow, Idaho. 172pp.

Swingland, I.R. 1983. Intraspecific differences in movement. Pages 102-115 in I.R. Swingland, and P.J. Greenwood, eds. The ecology of animal movement. Oxford Univ. Press, Oxford, Great Britain.

Terborgh, J. 1988. The big things that run the world. Conserv. Biol. 2:402-403.

Theberge, J.B., and C.H.R. Wedeles. 1989. Prey selection and habitat partitioning in sympatric coyote and red fox populations, southwest Yukon. Canadian J. Zool. 67:1285-1290.

Tinsley, J.B. 1987. The puma: legendary lion of the Americas. Texas Western Press, El Paso, Texas. 142pp.

Tomlinson, P.B. 1980. The biology of trees native to tropical Florida. Harvard Univ. Printing Office, Allston, Massachusetts. 480pp.

Toweill, D.E., and R.G. Anthony. 1988. Annual diet of bobcats in Oregon's Cascade Range. Northwest Science 62:99-103.

Treichler, R., R.W. Stow, and A.C. Nelson. 1946. Nutrient content of some winter foods of ruffed grouse. J. Wildl. Manage. 10:12-17.

Trewartha, G.T. 1943. An introduction to weather and climate. McGraw-Hill Book Co., New York, New York.

Tumilson, R., V.R. McDaniel, M.J. Harvey, M.L. Kennedy, and G.A. Heidt. 1982. A bibliography of bobcat literature. Arkansas Game and Fish Comm., Fed.Aid Wildl. Restoration Proj. No. W-56. 30pp.

Turkowski, F.J. 1980. Carnivora food habits and habitat use in ponderosa pine forests. U.S. Forest Service Research Paper, RM-215. 9pp.

TYDAC. 1991. SPANS spatial analysis system. Intera Tydac Technologies, Ottawa, Canada.

U.S. Dept. of Interior. 1979. Final supplement to the final environmental statement: phosphate leasing on the Osceola National Forest, Florida. Bureau of Land Manage., Alexandria, Virginia.

U.S. Fish and Wildlife Service. 1987. Florida panther recovery plan. Prepared by the Florida Panther Interagency Committee for the U.S. Fish and Wildl. Serv. Atlanta, Georgia. 75 pp.

U.S. Geological Survey. 1993. South Florida satellite map. U.S. Geological Survey, Denver, Colorado. 1pp.

Verspoor, E. 1983. Black bear predation on a mule deer fawn. Canadian Field-Naturalist 97:114.

Villarubia, C.R. 1982. Movement ecology and habitat utilization of black bears in Cherokee National Forest, Tennessee. M.S. Thesis. Univ. Tennessee, Knoxville, Tennessee. 159pp.

Voigt, D.R., and B.D. Earle. 1983. Avoidance of coyotes by red fox families. J. Wildl. Manage. 47:852-857.

Wade, D., J. Ewel, and R. Hoffstetter. 1980. Fire in south Florida ecosystems. U.S. For. Serv. Gen. Tech. Rept. No. SE-17. Southeast For. Exp. Stat., Asheville, North Carolina.

Walker, E.P. 1975. Mammals of the world. 3rd edition. Johns Hopkins Univ. Press, Baltimore, Maryland. 1500pp.

Waser, P.M., and W.T. Jones. 1983. Natal philopatry among solitary mammals. Quart. Review of Biol. 58:355-390.

Wassmer, D.A. 1982. Demography, movements, activity, habitat utilization and marking behavior of a bobcat (Lynx rufus) population in south-central Florida. M.S. Thesis, Univ. of South Florida, Tampa, Florida. 146pp.

Wassmer, D.A., D.D. Guenther, and J.N. Layne. 1988. Ecology of the bobcat in south-central Florida. Bull. Fla. State Museum Biol. Sciences 33:159-228.

Weaver, K.M., D.K. Tabberer, L.U. Moore, Jr., G.A. Chandler, J.C. Posey, and M.R. Pelton. 1990. Bottomland hardwood forest management for black bears in Louisiana. Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies 44:342-350.

Webb, S.D. 1974. Pleistocene mammals of Florida. Univ. Presses of Florida, Gainesville. 270pp.

Webb, S.D. 1984. Ten million years of mammal extinctions in North America. Pages 189-209 in P.S. Martin and R.G. Klein, eds. Quaternary extinctions- a prehistoric revolution. Univ. Arizona Press, Tuscon, Arizona.

Westfall, C.Z. 1956. Foods eaten by bobcats in Maine. J. Wildl. Manage. 20:199-200.

White, P.A., and D.K. Boyd. 1989. A cougar, Felis concolor, kitten killed and eaten by gray wolves, Canis lupus, in Glacier National Park, Montana. Can. Field Nat. 103:408-409.

Wing, E.S. 1965. Early history. Pages 5-12 in R.F. Harlow and F.K. Jones, eds. The white-tailed deer in Florida. Tech. Bull. No. 9. Florida Game and Fresh Water Fish Commission, Tallahassee, Florida.

Willey, C.H. 1978. The Vermont black bear. Vermont Fish and Game Department, Montpelier, Vermont. 74pp.

Williams, L.E. 1978. Florida panther. Pages 13-15 in J.N. Layne, ed., Rare and endangered biota of Florida. Vol. 1. Mammals. Univ. Presses of Florida, Gainesville, Florida.

Wilson, E.O. 1987. The little things that run the world (the importance and conservation of invertebrates). Conserv. Biol. 1:344-346.

Wilton, M.L. 1983. Black bear predation on young cervids- a summary. Alces 19:136-147.

Winegarner, C.E., and M.S. Winegarner. 1982. Reproductive history of a bobcat. J. Mammal. 63:680-682.

Winegarner, M.S. 1985a. Pugmarks and the biology of the bobcat (Lynx rufus). Z. Saugetierkunde 50:166-174.

Winegarner, M.S. 1985b. Bobcat family utilizes tortoise burrow. Fla. Field Nat. 13:32-33.

Wing, E.S. 1992. West Indian monk seal. Pages 35-40 in S.R.Humphery, ed. Rare and endangered biota of Florida. Vol. 1. Mammals. Univ. Press of Florida, Gainesville, Florida.

Witmer, G.W., and D.S. deCalesta. 1986. Resource use by unexploited sympatric bobcats and coyotes in Oregon. Canadian J. Zool. 64:2333-2338.

Wooding, J.B., and J.R. Brady. 1987. Black bear roadkills in Florida. Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies 41:438-442.

Wooding, J.B., and T.S. Hardisky. 1988. Black bear habitat study. Final performance report. Florida Game and Fresh Water Fish Commission, Tallahassee, Florida. 37pp.

Wooding, J.B., and T.S. Hardisky. 1990. Coyote distribution in Florida. Fla. Field Nat. 18:12-14.

Wooding, J.B., and T.S. Hardisky. 1992. Denning by black bears in northcentral Florida. J. Mammal. 73:895-898.

Wooding, J.B., S.M. Shea, M.L. Richardson, and D.Y. Dowling. 1992. Movements of a female black bear in northwestern Florida. Florida Field Nat. 20:46-48.

Woodruff, R.E. 1967. A giant palm weevil, Rynchophorus cruentatus (Fab.), in Florida (Coleoptera: Curculionidae). Entomology Circ. No. 63. Florida Dept. Agric. Gainesville, Florida.

Young, S.P. 1946. The wolf in North American history. Caxton Printers, Ltd., Caldwell, Idaho. 149pp.

Young, S.P. 1946. History, life habits, economic status, and control. Pages 1-173 in S.P. Young and E.A. Goldman, eds. The puma: mysterious American cat. Amer. Wildl. Inst., Washington, D.C.

Young, S.P., and E.A. Goldman. 1946. The puma: mysterious American cat. Amer. Wildl. Inst., Washington, D.C. 358pp.

Young, S.P., and H.H.T. Jackson. 1951. The clever coyote. Univ. of Nebraska Press, Lincoln, Nebraska.

Zezulak, D.S., and R.G. Schwab. 1979. A comparison of density, home range and habitat utilization of bobcat populations at Lava Beds and Joshua Tree National Monuments, California. Nat. Wildl. Fed. Sci. Tech. Ser. 6:74-79.

Zonneveld, I.S. 1990. Scope and concepts of landscape ecology as an emerging science. Pages 3-20 in I.S. Zonneveld, and R.T.T. Forman, eds. Changing landscapes: an ecological perspective. Springer-Verlag, New York, New York.

BIOGRAPHICAL SKETCH

David S. Maehr was born in Fairbanks, Alaska, on September 18, 1955 to Carol B. and Robert B. Maehr. He and his siblings, Brandt, Teddy, and Jenny grew up in Cincinnati, Ohio. David graduated from Walnut Hills High School in 1973 before attending the Ohio State University where he received his B.S. in wildlife management in 1977. During the 1970s, David worked as an artist for the Cincinnati Zoo, lead spelunking expeditions to Kentucky and Indiana, worked for the Ohio Environmental Protection Agency as a strip mine inspector, then as the Environmental Affairs Supervisor for a southeastern Ohio coal company. He married Diane Jo Sosnowski, from Uniondale, New York, on November 5, 1977. Following the recommendations of his good friend, Dr. Herbert W. Kale, II, David enrolled at the University of Florida where he obtained his M.S. in wildlife ecology in 1980. This work examined the effects of phosphate mining on north Florida bird communities.

David worked for the Florida Game and Fresh Water Fish Commission as a wildlife biologist from 1980 to 1994. This work produced over 30 refereed journal publications on the ecology of bobcats, black bears, Florida panthers, and north Florida avifauna, and created the foundation for the studies outlined in this dissertation, as well as for a forthcoming book about the biology and politics of Florida panther recovery. He is

also a co-author, with H.W. Kale, II, of the popular guide and handbook, Florida's Birds, which was published in 1990.

David is a Certified Wildlife Biologist, and serves on a number of advisory boards including the Endangered Cats of Texas and Arizona Recovery Team, the Florida Panther Technical Advisory Council, the Florida Committee on Rare and Endangered Plants and Animals (mammals), and the Florida Ornithological Society.

David is currently a senior biologist with Wilkison and Associates, Inc. in Naples, FL. In his spare time he is an avid swimmer, writer, and a lousy mechanic for an antique Bronco. Pen and ink drawing occasionally still occupies a few idle hours. David lives with his wife, Diane and two wonderful children, S. Clifton and Erin N., in western Collier County, Florida.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Lawrence D. Harris, Chair
Professor of Wildlife Ecology
and Conservation

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

John F. Eisenberg
Katharine Ordway Professor of
Ecosystem Conservation

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Melvin E. Sunquist
Associate Professor of Wildlife
Ecology and Conservation

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

John J. Mullahey
Associate Professor of Wildlife
Ecology and Conservation

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Elliott R. Jacobson
Professor of Veterinary Medicine

This dissertation was submitted to the Graduate Faculty of the Department of Wildlife Ecology and Conservation in the College of Agriculture and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

August, 1996

Dean, College of Agriculture

Dean, Graduate School