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Management of cougars (Puma Concolor) in the western United States

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MANAGEMENT OF COUGARS (*PUMA CONCOLOR*)
IN THE WESTERN UNITED STATES

A Thesis

Presented to

The Faculty of the Department of Biological Sciences
San Jose State University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science

By

Deanna Dawn

August 2002

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ABSTRACT

MANAGEMENT OF COUGARS (*PUMA CONCOLOR*) IN THE WESTERN UNITED STATES

By Deanna Dawn

In the U.S., cougar (*Puma concolor*) populations still exist in 12 western states. While sport hunting of cougars remains a management goal for 10 of these states, there is little information on how different hunting harvest strategies affect their biology. Both the rate of harvest and the percentage of females in the harvest affect population stability. Therefore, the purpose of this study was to examine the effect of different harvest strategies on the harvest rate and the percentage of females in the harvest. Annual hunting harvest records were requested from all 10 states and were summarized into a database for analysis.

Harvest strategies that included female sub-quotas were associated with the lowest percentage of females removed, however they also had some of the highest annual rates of harvest. These results suggest that, for some states, management strategies used in regulating sport hunting may offer little protection against over-harvesting the population.

DEDICATION

I dedicate this thesis to the biologists of the future:
Ellyn, Ethan, Bennett and Madeline.

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INTRODUCTION

At the most fundamental level, wildlife management implies stewardship of a population (Caughley and Sinclair 1994). Effective wildlife management depends upon obtaining reliable information about a species as well as incorporating that information into sound and testable management plans. With regard to cougars (*Puma concolor*), Hornocker suggested that management is the single most important factor in determining the welfare of the species (Nowak 1976). Sport hunting is the major mortality factor for cougars in most of the western U.S (Logan and Sweanor 2001), however, the impact of rapid removal of a large number of individuals from a population is not completely understood. Therefore, a periodic examination of harvest strategies is essential to understanding how decisions related to harvest programs may impact populations. It will also help to re-evaluate and redesign future harvest and management plans.

In the U.S., viable cougar populations exist in 12 states west of the Rocky Mountains. Management and regulatory control of these populations are mandated by individual states and vary from state to state. In 10 states, the hunting of cougars for sport is a primary component of management design. The state determines the parameters of the hunting season such as the number of hunters, the methods of take and the length of the season. The combination of

these variables produces the “harvest” which is in effect, the number of cougars removed by sport hunters.

The goal of this study was to summarize the history of cougar management in the U.S. and to examine the relationship between harvest strategies and harvest outcomes. The study begins by examining the historical relationship between humans and cougars. It reviews some of the changes in social factors that affected the distribution of cougars.

Designing an appropriate harvest strategy for cougars requires a fundamental understanding of their population dynamics. Despite cougars being hunted as a game species for more than thirty years, only two studies have experimentally examined the potential effects of sport hunting on cougar populations (Lindzey 1992, Logan and Sweanor 2001). The growth rate and viability of cougar populations are most likely affected by the loss of resident adult females and the level of harvest. Knowledge of these two components is necessary to evaluate the appropriateness of a harvest program, as well as, to determine the length of recovery of the harvested population. Therefore, the specific objective of this study was to examine the harvest strategies in the 10 western states and compare them to the annual harvest in order to identify changes in the harvest rate and gender composition of the harvest.

Historical distribution and influence of the bounty period

Prior to human settlement, cougars ranged throughout North and South America (Young and Goldman 1946). They have been known by many names including puma, mountain lion, panther, painter, catamount and leopardo (Hansen 1992). In North America, land development brought conflict between cougars and humans that ultimately led to a reduction in the number of cougars (Nowak 1976). Bounty payments were offered as incentives for the destruction of cougars and other predators. The earliest known bounty for cougars in North America began in the latter part of the 16th century (Young and Goldman 1944). During this time, Jesuit priests in Lower California offered a reward of one bull for each cougar killed.

Colonial settlers on the eastern coast also established legislation for the payment of bounties. On November 4, 1697, the General Assembly of West Jersey initiated the payment of 20 schillings for every cougar killed (Young and Goldman 1944). As land development began to spread west, so did bounties for cougars. Bounties were established in most states at one time or another and were paid from both public and private funds (Nowak 1976). By the late nineteenth century, cougars were already believed to be extinct in the eastern half of the United States. By 1920, the cougar's range was further reduced to the remote mountainous regions of the western states. In less than 300 years, intense hunting and loss of habitat have eliminated cougars from much of their historic

range, despite their previous existence in North America for more than 10,000 years (Culver et al. 2000).

Change in public sentiment towards cougars

An historical review of cougar management in the United States reflects a changing perspective regarding the role of this top carnivore. During the bounty period, cougars were considered vermin. Dislike of cougars was a response to the perceived threat they posed to livestock and human life. In a report on bounty hunting, J. S. Hunter wrote, "The one predatory animal for which practically no good can be said is the mountain lion" (California Fish and Game Department 1921). Jay Bruce (1922), a state mountain lion hunter for California wrote, "In fact, no animal in California is entirely exempt from the [mountain lion's] bloodthirsty instincts." Management during this time was, in effect, a widespread effort aimed at eliminating cougar populations.

By the 1960s, attitudes towards cougars changed significantly in North America (Nowak 1976). Although cougar populations had declined throughout much of the continent by this time, bounties were still paid primarily for the removal of depredating cougars. There was also an increasing interest in hunting cougars for sport. At the same time, there was a growing public appreciation and concern for the welfare of cougars and other large carnivores. Interests in both sport hunting and preservation prompted changes in

management. In 1965, the western states began reclassifying the cougar as a game species. This change in legal status reflected the changing sentiments, but more importantly, it represented the first form of legal protection for the cougar (Steve Torres, California Dept. of Fish and Game, personal communication).

The need for research

Reclassifying cougars as a game species presented a challenge to wildlife officials for they were now in charge of managing a species despite having only limited knowledge of its natural history. Much of the current understanding of cougar biology resulted from studies that began in the 1960s and 1970s (Hornocker 1967, Nowak 1976, Robinette et al. 1961, Seidensticker et al. 1973, Shaw 1977, Sitton and Weaver 1977). Since that time, the breadth of research has expanded considerably to include information such as surveying methods (Kutilek et al. 1983), home range size (Hopkins 1989), population characteristics (Logan and Sweanor 2001) and genetic structure (Culver et al. 2000).

Although cougars have been studied for more than thirty years, we still know relatively little about their behavior compared to other game species. Ironically, it is often the characteristics of its behavior that limit research possibilities. Cougars tend to occur at low densities over large areas so that a significant amount of time, effort and money is needed to locate and monitor individuals for study. They tend to be primarily nocturnal and crepuscular in

nature (Beier et al. 1995) and this greatly hinders direct observation of behavior. Lastly, cougars can have a natural life span of eight or more years, especially in un-hunted populations (Logan and Sweanor 2001, Hopkins 1989) therefore, financial constraints often prohibit research that covers an entire generation.

Power of public influence on management

Even if there were expanded knowledge of cougars it would not necessarily ensure wise management practices. This is due primarily to the influence that special interest groups have on management decisions (Wolfe and Chapman 1987). Currently, public opinion of cougars throughout the western United States is highly polarized. While ranchers are still concerned with protecting livestock from depredation, environmentalists may view the cougar as a symbol of wildness that warrants complete protection. Hunters may consider the cougar either as game or as a nuisance carnivore that preys upon desired game species. Conservation biologists may see the cougar as a keystone species whose presence indicates the overall health and integrity of an ecosystem.

Such diverse opinions result in regulations designed to satisfy people, not to manage cougar populations (Shaw 1989). Presently, cougars receive either complete, partial or no legal protection, depending upon the state. In most western states the cougar is listed as a game species and hunting is regulated by the state. In Texas however, the cougar is still considered vermin and its annual

harvest remains unregulated. In California, cougars are listed as a specially protected mammal and cougar hunting has not been permitted since 1972 (Torres 1996).

Principles of wildlife management

The success of any management strategy ultimately depends upon accurate and reliable information of the managed species. Since acquiring such knowledge is difficult at best, it is critical that wildlife managers consider the increased potential for error when designing management strategies for sport hunting of cougars. Strategies should be designed around specific and well-defined goals that are further refined into tangible objectives (Lindzey 1987). Objectives should be based upon measurable parameters gathered on a periodic basis that can be used to test the management strategy. The ability to monitor the degree to which these objectives are met ultimately determines the success of the management plan.

Long-term success of management policies depends on public support (McCullough 1979). The most appropriate management policy for any hunted species is biologically sound (e.g., ensures the continued existence of the species) and incorporates the needs of both consumptive and non-consumptive users. Revenue from the sale of sport hunting licenses, permits and ammunition has traditionally supported both habitat preservation and species research. Revenue

from non-consumptive users is often recently established and minimal. The danger in this situation is that those harvesting and those managing the resource become mutually dependant (Caughley and Sinclair 1994). This overlooks the concerns of non-consumptive users and turns a publicly owned resource into one that is managed for a single purpose, i.e., sport hunting.

Sustained yield

Leopold's (1933) *Game Management* ultimately became a cornerstone for species management. A fundamental component of Leopold's work was the concept of "harvestable surplus" or "sustained yield (SY)". Although developed for more traditional game species such as deer, this concept remains an underpinning in wildlife management today (McCullough 1979). In theory, it assumes that populations produce a surplus of individuals that can be removed without causing a population decline or extinction. The maximum amount of annual removal that a population can tolerate is known as the "maximum sustained yield (MSY)". Determining an appropriate level of either SY or MSY depends on knowledge of the population's growth and the relationship between the population and its resources (Caughley and Sinclair 1994). It also depends on the ability to accurately monitor trends in population size.

In theory, the concept of sustained yield makes sense, however, its application in management is limited by the ability to meet the criteria on which

it is based. The level of removal that a population can sustain depends in part, on the size of the population. Since there is no reliable method for enumerating cougar populations, managers lack critical information necessary for determining an appropriate level of sustained yield (Logan and Sweanor 2001).

In addition, sustained yield is essentially a model that, by its very nature, lacks the ability to account for both stochastic events and the dynamic nature of predator/prey relationships. It also does not account for exploitation that results in a population having a younger age structure or a disparate sex ratio, both of which can lead to a decrease in reproductive rate (Wolfe and Chapman 1987). Despite these limitations, the concept of sustained yield is still a fundamental component of cougar management.

Cougars as a game species

Bounties on cougars still existed in the western US until the late 1950s and early 1960s (Nowak 1976). Colorado and Nevada were the first states to classify the cougar as a game species in 1965, followed by Washington in 1966, Oregon and Utah in 1967, California in 1969, Arizona, Montana and New Mexico in 1971, Idaho in 1972 and Wyoming in 1973. By this time, the persistent pressure from bounty hunters, the growing interest in sport hunting, and the increased loss of habitat lead to a presumed decline in cougar populations.

Early management strategies attempted to stabilize these remaining populations, while still providing recreational opportunities for hunters and protection against livestock depredation. Through the early 1970s, most states had a general harvest season, in which the level of harvest was limited primarily by the bag limits (total number of cougars that can be killed per hunter in a harvest year) and the length of the season. Most states required hunters to purchase a cougar tag or permit. The annual harvest was usually estimated by some form of hunter survey.

By the mid 1970s, access to remote areas had increased along with an interest in sport hunting. This created the potential for over-harvesting of cougar populations. To address this issue, several states began to modify their harvest strategies. In 1972, cougars became a specially protected mammal in California and hunting was banned throughout the state. At the same time, research was beginning to provide new information regarding cougar natural history and population dynamics. The first mountain lion workshop was held in January 1976 and provided an opportunity for wildlife managers, biologists and other interested parties to share information regarding management strategies and research findings.

In the early 1980s, state agencies continued to increase efforts aimed at regulatory control of hunters and hunting harvest. Five out of 10 states had implemented harvest quota or limited entry systems. Several states placed

restrictions on the harvesting of females with dependent kittens. To increase recreational opportunities while still restricting harvest, "chase only" seasons were established in some states. In an attempt to address the issue of livestock depredation, some management plans redirected hunting efforts to areas of reported depredations. Collection of harvest data was also refined as mandatory checks of harvested animals replaced hunter survey methods.

In the early 1990s, all but two states were using some form of quota or limited entry season, with only Arizona and New Mexico retaining a general season strategy. The number of cougar licenses sold and the number of hunters in the field continued to rise in many states. Sub-quotas were implemented in three states (Idaho, Montana and Wyoming), which set further limitations on the number of females that could be harvested. In the mid 1990s, both Washington and Oregon banned the use of hunting hounds. As of 2000, Arizona was the only state to continue the use of a general season strategy.

Harvest strategies

Several issues are considered by state agencies when designing harvest plans for cougars. Management strategies may include goals of reducing pet or livestock depredations by cougars and increasing public safety in and around cougar habitat (Logan and Sweanor 2001). Reducing cougar predation on endangered species, such as desert bighorn sheep (*Ovis canadensis mexicana*), may

become a management objective in certain regions (e.g., Eastern Sierra in California).

Sport hunting is considered a means by which state agencies manage cougar populations (Washington Dept. of Fish and Wildlife 2001). The assumption is that appropriate harvest strategies will aid the state in this effort. However, since we cannot reliably monitor populations to evaluate the appropriateness of a given harvest strategy, we cannot determine the impact on the population. Therefore, game agencies are essentially managing the hunters, not the populations (Rick Hopkins, Live Oak Associates Inc., personal communication).

Description of harvest strategies

1. General season: This strategy allows for an unlimited number of individuals to be removed from the population during the hunting season. The length of the season is determined by the state. There is no restriction on the number of hunters allowed and no control of the ratio of males to females in the harvest.
2. Limited entry: This strategy limits the number of hunters allowed in a season. The season length is determined by the state. A state can limit the number of hunters it allows in a season by limiting the number of licenses it sells. An alternate strategy is to sell an unlimited number of licenses and then select, by lottery or drawing, a predetermined number from among those licenses that can

be used. Licenses usually allow for the removal of either males or females, however states may establish a proportion of licenses for male only removal.

3. Quota system: This strategy puts a legal limit on the number of animals removed in a season. Season length is determined by the state however, the season ends either when the quota is met or by the final season date. Quotas are set for either a total number of animals or for a total number of females. The season may be structured to remain open for "male only" harvest after the allowable number of females is removed.

Harvest strategies may be modified by adjusting the following parameters (states may also use a combination of harvest strategies to address specific goals within the state).

1. Season: The season length determines the total number of days that are available for hunting. Season length can be modified to increase or decrease sport hunting opportunities.

2. Hunting licenses: The number of licenses (permits or tags) sold determines the maximum number of hunters allowed during a hunting season. A state can choose to sell either a specific or an unlimited number of licenses per season. Licenses to hunt cougars may be sold individually or as part of a "sportsman's package" that contains licenses for several species. States may also establish separate license fees for in-state and out-of-state hunters. They may also set a limit on the number of out-of-state licenses they sell.

3. Hunt area: The size of hunt area determines the total amount of land that is legally available for sport hunting. The size of the hunt areas may be modified to increase or decrease sport-hunting opportunities. Hunt areas may be closed or opened in subsequent years to increase or decrease hunting opportunities or to distribute hunting pressure. Different areas within a state may have different management objectives therefore, harvest may increase in some areas and decrease in others. Removal of females may be restricted in some hunt areas but not in others. Road closures or access to hunt areas may be modified to increase or decrease hunting opportunities.
4. Harvest: The segment of the population that may be legally hunted. States may establish limits on the number of females or males that can be removed. States may also choose to protect certain age classes, such as kittens, and may either limit or prohibit the removal of females during certain times, such as when they have dependent young.
5. Hunting methods: The methods determine the ways that sport hunters can legally hunt cougars. Certain methods, such as the use of hounds or the use of traps, may be limited in all or some parts of a state. States may allow certain methods and restrict others to increase or decrease hunting opportunities.

Theoretical control of harvest

Theoretically, changing from a general to a quota or limited entry season improves the regulatory control of hunters and harvest. This should also increase protection against over-harvesting the population. Opinions regarding the potential effect of harvest strategies on the populations vary. Quota systems attempt to limit the harvest to some predetermined number. This system may reduce potential over-harvesting during years of unusually favorable hunting conditions (i.e., increased snowfall) or in areas that are easily accessible to hunters (Tom Beck, Colorado Division of Wildlife, personal communication).

It is also possible that competition for a limited resource reduces hunter selectivity. This could increase the take of females or younger aged animals, or both. A reduction in selectivity for males may increase even further as total take approaches the quota. When quotas are established only for selected units within a state, hunters may shift their efforts to the less restrictive areas, thereby increasing the potential to over-harvest certain populations (Lindzey 1987). Quota systems may also increase the under-reporting of harvested animals. This may occur when animals are knowingly or unknowingly harvested after quotas have been filled. Additionally, if quotas apply only to specific areas, hunters may continue to hunt these areas but report their kills as originating from outside the quota unit. Under-reporting may increase when sub-quotas for females are established. Females killed after the female sub-quota has been

reached (usually by misidentification) are considered illegal, and may be abandoned as the hunter continues to pursue a male.

Limited entry systems control the number of hunters allowed to hunt in a season. This can potentially reduce hunter overcrowding in areas with easy access (Tom Beck, Colorado Division of Wildlife, personal communication) and may also increase hunter selectivity for males since pressure between hunters for a limited resource is reduced. Limiting the number of hunters may also decrease the number of hunting hounds used in a season. This could benefit cougar and other wildlife populations by reducing the disruption caused by hounds. Limited entry seasons place no restrictions on gender therefore, a disproportionate number of females or males, may be removed especially if an area is easily accessible to hunters.

This study examines the relationship between the hunting harvest and harvest strategies. The rate of harvest as well as the percentage of females in the harvest is calculated from harvest data for all 10 states. The purpose of this study is to determine if these two components of the harvest vary among states that are using different harvest strategies.

METHODS

The 10 states included in this study were Arizona, Colorado, Idaho, Montana, Nevada, New Mexico, Oregon, Utah, Washington and Wyoming.

Sport hunting is prohibited in California and unregulated in Texas therefore these states are not included in this analysis.

In order to assemble a database, an outline of the study objectives and a request for hunting harvest data was sent to the cougar/furbearer coordinator in each state. Supplemental information was obtained from Federal Aid Reports, Fish and Game annual reports and from the proceedings of the six mountain lion workshops. Once the harvest information was extracted from the documents obtained, it was returned to the state coordinator for final review.

All of the analyses were derived from the assembled database. The first analysis examined the harvest in all 10 states regardless of harvest strategy for the last 30 years. Linear regression analysis was used to determine if the annual harvest of cougars in each state changed linearly overtime. To more closely examine when changes in harvest rates occurred, a series of five-year harvest averages for each state were compared to the average harvest occurring prior to 1980. Gender data for most states did not become available until the early 1980s, which precluded any analysis of the potential relationship between harvest rate and the percentage of females removed for the entire 30-year period. However, an annual average of the percentage of females in the harvest for all 10 states was calculated.

The second analyses examined the removal that occurred in each state as a result of using different harvest strategies. Linear regression was used to

determine both the rate of removal and if the removal occurred linearly over time. The average percentage of females in the harvest for each strategy was also determined.

The final analysis examined the four most common harvest strategies. Harvest rates were compared to the percentage of females in the harvest. A one-way Kruskal Wallis test was used to determine if there was a significant difference in the percentage of females in the harvest among the four strategies.

Harvest totals for all analyses were calculated by harvest year, which may or may not have coincided with the calendar year. All analyses were performed using SPSS version 11.0.

RESULTS

With the exception of Washington, all states had a significant linear increase (as reflected in a positive slope for the regression equation and a p-value of less than 0.05) in the number of cougars harvested annually over the last 30 years (Table 1). By 1990, eight out of 10 states increased their annual harvest from 57-584 % relative to the take occurring before 1980 (Fig 1A, B). Two states, Arizona and Washington, decreased their average annual harvest (compared to the average take prior to 1980) for this period. By 2000, all 10 states had increased annual harvests relative to 1980, with average increases between 15-1252 % (Appendix 1).

Most importantly, in the last decade harvest totals nearly doubled in Colorado, Utah, Washington and Wyoming compared to the period between 1980 and 1990. Idaho increased its harvest by nearly two and half times while Montana's totals increased by more than three and a half times.

Since the mid 1980s, several states have initiated regulations to limit or reduce the number of females in the annual harvest. Between 1981 and 1989, the percentage of females in the harvest for all states never rose above 44%. Over the past decade, the percentage of females in the harvest has steadily increased, reaching 48% in 1999 and 2000 (Fig 2). The states that contributed most to this increase were Idaho, Montana, Oregon, Utah, Washington and Wyoming. Only Nevada and New Mexico had relatively consistent rates of females in their harvest for this period.

Rate of harvest by harvest strategy

Linear regression analysis determined the rate (slope of the linear regression equation) of harvest in all states using the following harvest strategies: general, quota, limited entry, combined strategies and restricted hound seasons. A period of three consecutive years was established as the minimum for this analysis. With a general harvest season, Arizona, Idaho, Montana and Utah had significant increases in harvest (as reflected in a positive slope for the regression equation and a p-value of less than 0.05 (Table 2A). Washington was the only

Table 1. Results of linear regression analyses of annual hunting harvest for cougars in the western United States.

States	years	n (# of years)	slope of regression equation	r ²	p-value
Arizona	1971-2000	30	2.13	0.17	≤0.05
Colorado	1970-2000	31	12.63	0.90	≤ 0.05
Idaho	1972-2000	29	23.81	0.83	≤ 0.05
Montana	1971-2000	30	23.81	0.83	≤ 0.05
Nevada	1970-2001	32	3.83	0.53	≤0.05
New Mexico	1972-1999	28	3.96	0.74	≤0.05
Oregon	1970-2001	32	5.28	0.59	≤ 0.05
Utah	1970-2001	32	12.27	0.80	≤ 0.05
Washington	1973-2000	28	0.97	0.02	0.48
Wyoming	1975-2000	26	6.54	0.853	≤ 0.05

Figure 1. Five year average for the number of cougars killed by sport hunters in the Western United States through 2000.

Figure 2. Percentage of female cougars in the sport hunting harvest in the Western United States from 1981-2000. Data represent the average percentage of females in the annual harvest for all states.

Table 2. Results of linear regression analysis for hunting harvest of cougars using different harvest strategies.

A. General					
State	Arizona	Colorado	Idaho	Montana	Nevada
years	1971-2000	1965-1969	1983-1990	1971-1985	1970-1975
n	30	5	8	15	6
slope	2.13	9.10	9.13	6.35	-5.63
r ²	0.17	0.71	0.41	0.70	0.26
p value	≤ 0.05	0.07	≤ 0.05	≤ 0.05	0.3
State	New Mexico	Utah	Washington	Wyoming	
years	1972-1998	1967-1977	1966-1986	1975-1979	
n	27	11	21	5	
slope	3.95	8.99	-7.13	2.50	
r ²	0.72	0.40	0.53	0.32	
p value	0.30	≤ 0.05	≤ 0.05	0.32	
B. Quota					
State	Colorado	Colorado	Nevada	Wyoming	
years	(1975-1979) ¹	(1980-2000) ²	(1981-2001) ²	(1980-1992) ²	
n	5	21	21	13	
slope	-0.60	16.19	3.55	3.62	
r ²	0.01	0.89	0.29	0.50	
p value	0.89	< .05	< .05	< .05	
State	Montana	Wyoming	Montana		
years	(1988-1993) ³	(1993-2000) ³	(1994-2000) ⁴		
n	6	8	7		
slope	54.14	15.27	17.89		
r ²	0.91	0.83	0.18		
p value	≤ 0.05	≤ 0.05	0.35		
1- total quota + male quota					
2- total quota					
3- total quota + female quota					
4- total quota + female quota + male quota					
C. Limited entry					
State	Oregon	Nevada	Utah	Washington	
years	1970-1995	1976-1980	1989-1995	1987-1995	
n	26	5	6	9	
slope	7.77	7.90	34.89	21.10	
r ²	0.85	0.79	0.82	0.76	
p value	≤ 0.05	≤ 0.05	≤ 0.05	≤ 0.05	
D. Combined strategies					
State	Idaho	Utah	Utah		
years	(1991-2000) ¹	(1979-1988) ²	(1996-2000) ³		
n	10	10	5		
slope	46.92	-0.93	-15.57		
r ²	0.72	0.01	0.19		
p value	≤ 0.05	0.74	0.39		
1- female quota + general season					
2- general season + limited entry					
3- total quota + limited entry					
E. Use of hunting hounds prohibited					
State	Oregon	Washington			
years	1996-2001	1997-2000			
n	6	4			
slope	30.66	31.70			
r ²	0.81	0.49			
p value	≤ 0.05	0.30			

state that had a significant decrease (a negative slope for the regression equation).

Under a total quota system (limiting the total number of removals, no restriction on gender) Colorado, Nevada and Wyoming all had significant increases in harvest (Table 2B). When a quota system included a sub-quota on the number of females that could be removed, both Montana and Wyoming had significant increases in harvest. Harvests did not increase significantly in Colorado or Montana when quota systems included additional sub-quotas for males, females or both sexes.

With limited entry seasons, Oregon, Nevada, Utah and Washington all had significant increases in harvest (Table 2C). When Idaho used both a general season and female sub-quotas in alternate parts of the state, it had an overall significant increase in harvest (Table 2D). When Utah combined limited entry seasons with quota or general seasons, there was no significant increase in harvest. When the use of hunting hounds was eliminated, Oregon had a significant increase in harvest while Washington did not (Table 2E).

Percentage of females removed by harvest strategy

The average percentage of females harvested with each harvest strategy varied from 32-60% among the states (Table 3). Among the four most commonly

Table 3. Average percentage of female cougars in the sport harvest using different harvest strategies.

State	Harvest strategy	years	n	ave. % Female
Arizona	General	1982-2000	19	46
Colorado	Quota (T+ M) ¹	1975-1979	5	42
"	Quota (T) ²	1980-2000	17*	43
Idaho	General	1983-1990	8	43
"	Quota (F) ³ + General	1991-2000	10	42
Montana	General	1971-1985	15	40
"	Quota (T + F) ⁴	1988-1993	6	32
"	Quota (T + F + M) ⁵	1994-2000	7	47
Nevada	General	1970-1975	6	53
"	Limited Entry	1976-1980	5	44
"	Quota (T) ²	1981-2001	21	41
New Mexico	General	1981-1998	18	39
Oregon	Limited Entry	1987-1994	8	40
"	Quota (T) ² No Dogs	1996-2001	6	48
Utah	General + Limited Entry	1979-1988	8	37
"	Limited Entry	1989-1995	7	34
"	Quota (T) ² + Limited Entry	1996-2001	6	45
Washington	General	1973-1986	10**	48
"	Limited Entry	1987-1995	9	44
"	General No Dogs	1996-2000	5	60
Wyoming	General	1975-1979	5	39
"	Quota (T) ²	1980-1992	13	46
"	Quota (T + F) ⁴	1993-2000	8	42

n = total # of years

* data not available 1984-1987

** data not available 1980-1983

1-quota for total and for total number of males

2-quota for total only

3-quota for females only

4-quota for total number and for total number of males and females

Figure 3. Percentage of female cougars in the sport harvest in the western United States using the four most common harvest strategies. Data represent the average percentage of females for each harvest strategy. A one-way Kruskal Wallance analysis tested for differences among the four harvest strategies (corrected for ties, $df=10$, $p = 0.05$).

* quota for total harvest only

** quota for total harvest and total female harvest

used harvest strategies, general seasons and total quota systems (restricting the total harvest only) had similar percentages of females in the harvests (Fig 3). The percentage was lower with limited entry systems. Quota systems that placed additional sub-quotas on the number of females removed had the lowest average percentage of females in the harvest. A one-way Kruskal Wallis test revealed a significant difference in the percentage of females in the harvest among the four most commonly used harvest strategies. Nonparametric multiple comparisons determined there was a significant difference between the percentage of females in the harvest with general seasons and quota systems using female sub-quotas (d.f.=3, SE=14.854, $p < 0.05$).

A comparison of the four most common harvest strategies revealed that general seasons had the lowest rate of harvest (Table 4). Limited entry and quota systems that limited only the total take had intermediate rates. Quota systems with female sub-quotas had the highest rates of harvest. The percentage of females in the harvest was lowest when the harvest strategy included female sub-quotas.

DISCUSSION

The results of this study found that general harvest seasons produced the slowest rates of harvest among the harvest strategies. General seasons were most commonly used shortly after the end of the bounty period when cougar

Table 4. Harvest rates and the percentage of females in the harvest with the four most common harvest strategies in the western United States. States with a positive linear increase in harvest (slope > 0) are compared to the percentage of females in the harvest during the same period.

State	Harvest strategy	years	n (# of years)	percent female*	slope**
Arizona	General	1982-2000	19	46	7.52
Idaho	General	1983-1990	8	43	9.13
Montana	General	1971-1985	15	40	6.35
Nevada	Limited Entry	1976-1980	5	44	7.90
Utah	Limited Entry	1989-1995	7	34	34.89
Washington	Limited Entry	1987-1995	9	44	21.10
Idaho	Quota (F) + General ¹	1991-2000	10	42	46.92
Montana	Quota (T + F) ¹	1988-1993	6	32	54.14
Wyoming	Quota (T + F) ¹	1993-2000	8	42	15.27
Colorado	Quota (T) ²	1980-2000	17*	43	16.19
Nevada	Quota (T) ²	1981-2001	21	41	3.55
Wyoming	Quota (T) ²	1980-1992	13	46	3.62

* percentage of females in the harvest

** slope of the linear regression equation

1-quota for females only

2-quota for total only

numbers were presumed to be significantly reduced throughout the United States (Nowak 1976). This relatively low rate of harvest may have reflected reduced populations of cougars in some regions. At that time, there was a relatively low interest in sport hunting of cougars. Harvest totals during that time were primarily estimates based upon hunter surveys therefore, actual harvest totals may have been different.

In hunted populations, harvests rates may increase for several reasons. There is a strong correlation between the number of cougars killed and the number of hunting licenses sold (Logan and Sweanor 2001, Final EIS Montana Fish, Wildlife and Parks 1999, Utah Div. of Wildlife Resources 1999). Harvest rates may also increase when states liberalize restrictions on harvest (i.e., increasing annual quota numbers).

Regardless of the cause, increasing harvests do not necessarily represent increasing cougar populations; they may simply reflect the level of hunting effort that is allowed in a season. Favorable snow conditions and increased technology (i.e., cell phone communication, telemetry equipment used on hunting hounds, snowmobiles, etc.) improve the hunter's ability to locate cougars (Kenneth Logan, Wildlife Health Center UC Davis, personal communication). Reducing the cost of cougar permits may increase the number of in-state and out-of-state hunters. Incidental take of cougars (e.g., opportunistic removal by deer and elk

hunters) may increase when cougar tags are included as part of a sportsman's package.

This study also found that the percentage of females in the harvest differed significantly among the four most common harvest strategies. The number of females in any harvest may increase, in part, due to the difficulty in determining gender. Adult cougars are not clearly dimorphic therefore, gender may be misidentified, especially by inexperienced hunters. A recent study in Wyoming found that with in-hand dead cougars, gender was misidentified 9% of the time (Anderson and Lindzey 2000). Track and body sizes of adult females are similar to those of sub adult males. This may make identifying gender in heavily hunted populations especially difficult due the increased number of younger aged animals (Lindzey 1987).

Most hunts are initiated from tracks found in the snow. Since track size is not a reliable indicator, hunters pursue cougars before they make a definitive determination of gender. Hunters may be more inclined to harvest an animal regardless of its gender when a hunt has taken a considerable amount of time or when the end of the season or the filling the quota is near. In heavily hunted populations, an increasing take of females can indicate that previous hunting efforts have significantly reduced the number of males. Regardless of the cause, increasing numbers of females in the harvest may indicate that the population cannot withstand the current rate of harvest (Lindzey et al. 1992).

Potential effects of sport hunting on cougar populations

To better understand how cougar populations may be impacted by harvest strategies, it is critical to consider their metapopulation structure (Logan and Sweanor 2001). Cougar metapopulations are distributed heterogeneously throughout the western states based on differences in the size of habitat patches, the level of connectivity between the patches, habitat quality and prey availability. An analysis of statewide harvest totals offers no insight into how metapopulations are affected by sport hunting.

Only two studies have experimentally examined how cougar populations respond to a simulated harvest. In Utah, biologists experimentally removed 27% of the harvestable population (> 1 year old) (Lindzey et al. 1992). Two years after this removal, the adult resident female population had still not fully recovered.

In New Mexico, an experimental population was reduced by 47% (adult segment of the population was reduced by 53% and sub-adults were reduced by 58%) (Logan and Sweanor 2001). It took 31 months for the adult segment of the population to fully recover to pre-harvest densities. Results from both studies suggest that similar annual rates of harvest would not be sustainable for cougar populations inhabiting similar environments.

Previous harvest totals are commonly evaluated when determining harvest objectives for the following year. When annual harvest totals remain constant this creates the false impression that similar rates would be appropriate for the

future. It is even more dubious to use consistent harvest rates to justify an increase in harvest objectives in the future. This creates what Logan and Sweeney (2001) term the "sledgehammer effect." Harvest rates continue to increase thereby hammering the population into a decline. The first indication of a decline may occur when hunters and houndsmen start to complain about the lack of available animals to harvest. Given the increasing rates of harvest over the past 10 years, it is possible that harvest strategies in many states are creating just such a situation.

In cougar populations, recruitment is necessary for population stability. In both the Utah and New Mexico studies (Lindzey et al. 1992, Logan and Sweeney 2001) recruitment patterns were similar. Both progeny and immigrants (cougars originating from outside the study area) replaced adult females, while male recruitment was based principally on immigration. Therefore, metapopulations are dependant on some level of migration between subpopulations to maintain their population persistence. Hunting impacts this component of population dynamics differently for males and females. When a resident adult male is removed from the population, breeding opportunities may be reduced for the females within his home range. Cub survival may also be reduced as a result of infanticide by incoming males, but the frequency of this occurrence is unknown. In severely isolated populations, where immigration of new males is limited, loss of a resident adult male can significantly reduce reproduction (Beier 1993).

Loss of adult females can significantly impact the population by reducing reproduction. Many states provide legal protection for females with dependant cubs, however this regulation may be largely ineffective since identifying a female who is raising cubs is difficult. Barnhurst and Lindzey (1989) found that tracks of kittens less than 7 months old are encountered along with their mothers less than 20% of the time. In addition, during the first year, mothers may hunt for several days without returning to their kittens (Lindzey 1987). Females can produce kittens year round and as many as three out of four females may have dependant cubs. Distended teats are only visible for approximately two months and are not reliable indicators of dependant young. Cubs orphaned at less than nine months old are unlikely to survive (Logan and Sweanor 2001). These factors, combined with difficulties in identifying gender, offer no real safeguard against the removal of females with cubs.

Female cougars seem to be largely philopatric, therefore daughters often serve as replacements after the loss of their mother. When removal of adult females is light, impact to the population may be minimal, providing there are enough sub-adult females available to compensate for the potential loss in reproduction. In situations where the removal of adult females is relatively high, populations may decline due to reduced recruitment potential.

Hunting losses may be largely additive to other sources of mortality (Lindzey et al. 1992). Harvest figures represent only the number of cougars

killed by hunters that are reported to the state and constitute the minimum mortality from hunting efforts. Additional mortalities attributed to hunting include the killing of kittens or adults by hunting hounds, the starvation of kittens after removal of their mother and injuries sustained during pursuit leading to subsequent death and illegal killings. These mortalities cannot be predicted or controlled, and may be excessive in heavily hunted populations. Additionally, these mortalities will most likely go unrecorded and will not be part of the determination of hunter impact.

Theoretically, harvest strategies provide recreational opportunities for hunters while providing protection against over-harvesting. The data presented here suggest that current harvest strategies do little to prevent over-harvesting, and in some states, they may be testing the limits of a population's ability to withstand it.

The rate of harvest is controlled primarily by the number of hunters allowed in a season. Reducing the percentage of females in the harvest is best achieved with the use of female sub quotas, however the observed increase in harvest rate with this strategy creates additional potential for over-harvest. Therefore, a limited entry season combined with sub-quotas on females, would offer the best compromise among the current harvest strategies. This assumes however, that the number of hunters and sub-quotas is conservatively set and there is ongoing research within the state to study the potential impacts of

hunting. Funds (e.g., from the sale of hunting licenses) should be appropriated on an annual basis specifically for this purpose. Even though this more restrictive harvest strategy provides additional protection for cougars, without a reliable method to census their populations, managers cannot be assured that it will maintain population stability. The proposed strategy would reduce sport hunting revenue (limited number of hunting licenses sold, funds appropriated for research) therefore, it is unlikely to be implemented without a change in attitude and outlook regarding the conservation of cougar populations.

An alternate management strategy proposed by Logan and Sweanor (2001) and based on metapopulation theory (Meffe and Carroll 1994), offers the best approach to managing cougars while still providing sport hunting opportunities. The "Zone Management System" essentially divides the suitable habitat within a state into zones according to specific management objectives. Hunting zones would be established to provide recreational opportunities for hunters. Other areas of the state where hunting would be prohibited would be designated as refuge zones. Refuge zones would create a source population from which individuals can disperse to replenish the sink populations that are likely to be created by hunting zones. Refuge zones are necessary to account for the uncertainty in results of management objectives in other zones. Refuge zones would also allow for natural selection to be paramount in a population instead of the human selection that occurs when cougars are hunted. Control zones would

be areas where the increased removal of cougars is deemed necessary to reduce livestock depredations or increase public safety. Sport hunting efforts in control areas would provide additional recreational opportunities while reducing the cost to taxpayers by minimizing the number of removals made by government agents.

In hunting zones, the total harvest should not exceed the populations' rate of increase. Logan and Sweanor's (2001) work in New Mexico provided the longest time span for which the rate of increase was determined for a cougar population. For adult cougars they estimated a maximum observed rate of increase of 11% and 28% per year for a protected and an experimentally reduced population, respectively. Based on their findings they recommend that initial harvest should not exceed 8% of the adult male population. A relatively low rate of harvest allows for the uncertainties in estimating population size while providing a buffer of protection against the influence of stochastic events.

Logan and Sweanor (2001) also recommend that females and kittens remain protected but that modest quotas for females are established to address issues of gender misidentification. This would help to minimize under-reporting of female kills that occur with other harvest strategies.

Finally, they recommend that specific objectives be defined for each zone, and management in each zone be conducted as a biological experiment. Determining the manner in which management objectives are met could provide

a better understanding of how cougar populations respond to human manipulation. Conversely, failure to meet objectives could encourage new and creative approaches to management.

The "Zone Management System" offers many benefits over more traditional harvest strategies. It can reduce the potential for over-harvesting by creating refuge zones. It can contribute to a better understanding of cougar population dynamics through the merging of management and research. Finally, it can address the desires of a broader segment of the public by simultaneously allowing for hunting, depredation removals and non-consumptive uses.

The effectiveness of any management plan depends upon its design and execution. These components are ultimately rooted in the values and opinions of those involved in the making management decisions. For cougar populations to persist in the future, knowledgeable managers need to be supported by an unbiased Game Commission.

Cougars, like all wild species, are a publicly owned resource. This means that all residents within a state should have an equal say in determining their fate. Due to lack of information, understanding or interest, this is not the case. Until such time that the scale of influence is more equally weighted, it is likely that management will continue to be strongly influenced by sport hunters and live stock owners.

Like all large carnivores, cougars help to insure the integrity and functioning of the environments in which they live. Managing cougars will continue to provide challenges, however, if we aspire to maintain healthy ecosystems, we must recognize that proper management of all wildlife is fundamental to this undertaking.

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Appendix 1. Compiled Hunting Data From 10 Western States.

Contains five-year averages and percentage changes in the number of cougars killed by sport hunters. The percentage change is the average harvest for each five-year period relative to the average harvest occurring prior to 1980.

	Arizona		Colorado		Idaho		Montana	
ave. to 1980	208		57		110		73	
	5 year ave.	% change	5 year ave.	% change	5 year ave.	% change	5 year ave.	% change
1981-1985	161	-22.8	126	121.1	201	82.5	133	82.2
1986-1990	176	-15.2	187	228.8	287	160.7	174	137.8
1991-1995	207	-0.4	293	414.4	437	297.1	424	480.3
1996-2000	264	27.1	374	556.8	703	538.7	662	806.6
	Nevada		New Mexico		Oregon		Utah	
ave. to 1980	48		62		21		139	
	5 year ave.	% change	5 year ave.	% change	5 year ave.	% change	5 year ave.	% change
1981-1985	80	65.8	108	74.5	57	171.4	191	37.4
1986-1990	104	116.3	98	58.1	144	583.8	218	57.1
1991-1995	148	209.2	124	100.0	137	550.5	332	139.0
1996-2000	136	182.9	155	149.4	111	430.5	465	234.0
	Washington		Wyoming					
ave. to 1980	169		12					
	5 year ave.	% change	5 year ave.	% change				
1981-1985	111	-34.3	41	245.0				
1986-1990	100	-40.6	70	483.3				
1991-1995	168	-0.5	80	568.3				
1996-2000	195	15.4	162	1251.7				