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Managing puma hunting in the western United States: through a metapopulation approach

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Abstract

To achieve long-term viability of hunted puma (*Puma concolor*) populations (even at historically low densities), we propose a management plan based on the metapopulation concept that designates *source areas* (closed to hunting) and *sink areas* (open to hunting). We use 11 years of data from Idaho and Utah to demonstrate how the proposed management plan might be implemented. We use minimum and maximum densities of resident animals to calculate minimum and maximum effective population sizes, neighbourhood areas (regional management units) and usable habitat within the units. We designate sink and source areas based on their size, accessibility to hunters and juxtaposition. We show that closing 63% of puma habitat to hunting would ensure long-term puma population viability while permitting traditional hunting levels in other areas. This system could be adapted to existing state (and interstate) hunting management units, and we outline several steps by which wildlife agencies might set up a process (including public participation) to manage puma hunting.

INTRODUCTION

Prior to about 1960, the management goal for pumas and other large carnivores in the western states was elimination (Gittleman *et al*., 2001). Pumas (also called mountain lions or cougars) were viewed as dangerous competitors, killers of livestock and game animals, and threats to safety (Hansen, 1992; Deurbrouck and Miller, 2001). In the 1960s many states gave them 'game' status which afforded limited protection (Hansen, 1992). Today, however, pumas are recognized conservation keystone, indicator or umbrella species that reflect the ecological health of an area (Kellert & Smith, 2000). With this new image and their limited numbers (e.g. estimates of Idaho's total population range from 2000 to 4000 animals), the hunting of pumas has become controversial.

Even within the hunting community, many feel that current management plans do not protect pumas from over-hunting and point to alarming trends in recent harvest levels. For example, Idaho's annual harvest rate increased from 330 animals/year in 1992 to approximately 700 animals/year in 1995–99 (Idaho Fish and Game Department, 2001) despite the lack of data on the status of puma populations and how the public wants pumas managed. The same is true in Wyoming and elsewhere (e.g. Mangelsen, 2000) and there have been successful efforts to eliminate hunting of this species, e.g. California (Torres *et al*., 1996), or limit the effectiveness of hunters by banning the use of dogs (Washington Department of Fish and Wildlife, 1999).

On the other hand, there is growing concern for human safety from puma attacks (Beier, 1991, 1992; Deurbrouck & Miller, 2001), attributed to a perceived increase in puma numbers and human encroachment on puma habitat. Also, there is a growing consensus that pumas are the cause of a recent decline in mule deer (*Odocoileus hemionus*) numbers (Murphy, Ross & Hornocker, 1999; Unsworth *et al*., 1999; Ballard *et al*., 2001). Many argue that hunting is a necessary management tool for the control of human/puma conflicts and to aid mule deer populations. The perspectives people have on these matters may determine the kind of puma management that is politically possible (see Clark *et al*., 2001; Clark, 2002).

Conflict among the various interest groups is increasing. Many people view the current management process as biased towards hunting interests and embedded in state's-rights power issues (e.g. Mangelsen & Blessley, 2000). Others argue that decisions, whatever their direction, are being made without adequate knowledge. What data do we have to support or refute the claim that hunting endangers puma populations (Murphy *et al*.,

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1999), or that lack of hunting provides an environment for increased puma attacks? Clarification of the overall management goals for pumas and the role of hunting in attaining those goals is badly needed.

The goals of this paper are (1) to review the management of puma hunting within one study area in southeastern Idaho and northwestern Utah and (2) to suggest an alternative example of how the metapopulation concept can be used to sustain viable puma populations over the long term while allowing historic hunting levels. To accomplish these objectives, we use data from other studies and from our 16-year Idaho puma study (Laundré, 2000; Laundré & Hernández, 2000), ongoing efforts to find acceptable puma management policy in western Wyoming, and records from puma management elsewhere. Finally we offer guidelines to managers on how to implement the alternative plan proposed and reduce conflicts among interest groups. Our overall purpose is to assist in defining puma and large carnivore management policy in the public interest.

Controversy over management of hunting

The goal of any puma management plan should be to ensure the long-term survival of the species (Ross, Jalkotzy & Gunson, 1996). For conservation management, this goal is achieved by addressing minimum viable populations, long-term population viability, habitat protection and connectivity among subpopulations. Where puma hunting exists, this goal is embedded in strategies such as sustainable yields, target population sizes, bag limits and hunter success. Although these two approaches speak different languages, their overall management goal remains the same – long-term survival of the species. Here we adapt a management goal for pumas assuring sustainable populations for > 100 years and we then assess hunting of pumas to see if it meets this goal.

Until about 1970, pumas were considered 'varmints' by state and federal agencies, and in all areas a bounty was paid for killing them (Hansen, 1992). In the early 1970s most states, except Texas, elevated the status of pumas to 'game', and established seasons and restricted take to adult males and adult females without kittens. Within these regulated seasons, there are currently three approaches to the hunting of pumas.

The first we call *open hunting* because, within the season (usually ~6 months), there is no restriction on the number of qualifying animals that can be killed apart from the number (usually one) that an individual hunter can kill. The state is usually divided into a series of management units, and within those units all areas are open to all hunters for the length of the season. The limit on the number of pumas killed in an area is determined primarily by the number of hunters and the accessibility of the area. Second is the *permit system*, in which a certain number of permits are issued per management unit and allocated to hunters through a lottery. The number of permits is based in theory on some estimate of the puma population in each unit. However, there is no way to estimate puma populations accurately (Smallwood, 1997; Choate, Wolfe & Belovsky, 2000; Gratson *et al.* 2000), so in reality the number of permits is based on someone's 'best guess,' past harvest success or – all too often – local politics. Under this system, the maximum number of animals that can be killed is equal to the number of permits issued. Third is the *quota system*, under which the season closes for a unit when a certain number or quota of animals, usually females, has been killed (Ross *et al.*, 1996). Until that number of qualifying animals is killed, there is often no limit on the number of other animals, usually males, that can be killed. The basis for deciding the quota number is the same as for the permit system. Under this system, the minimum number of animals that can be killed depends on the success of the hunters or the quota of qualifying animals, and, theoretically, there is no maximum limit on the number of males that can be killed.

To understand why there is controversy over these various management approaches, we need to consider each, relative to the goal of long-term survival of viable populations. In the open-hunting system, there is minimal control on the timing and length of the hunt because these seasons usually are long (~6 months) and are held in winter to maximize success. Within the hunting season, there is no limit on the take, so that given the right conditions, e.g. abundant snowfall, local puma populations can be severely over-hunted. In the past, the chances of over-harvesting were low because of the low number of puma hunters and the limited accessibility to many areas. However, the number of hunters continues to increase dramatically (Lindzey *et al.* 1989; Wolfe, Bates & Choate, 2000), and the use of snowmobiles and ATVs has increased accessibility significantly. For these reasons, open hunting offers little security to the long-term survival of pumas.

For both the quota and the permit approaches, there is more control on the number of animals that can be killed. The permit system offers more control in that a specified maximum number of pumas can be harvested, equal to the number of permits issued. The quota system is not as precise; it specifies a maximum number of selected animals but does not limit the number of other animals that can be killed as long as the maximum of selected animals is not met. Although both approaches provide tighter control, selecting the number of permits or the quota level is still based on estimates of population numbers or, as mentioned, purely political motivations. For example, in the two state management units included in our study area in Idaho, the female quota has ranged from two to nine over the last 6 years (Idaho Fish and Game, Mountain Lion Hunting Regulations, 1994–2000). During that time, based on intensive fieldwork, our estimates of population numbers in these units ranged from 20 to 34 adults, residents and transients (Laundré & Hernández, 2000). However, there has been no relationship between population numbers and quota levels. On the contrary, the highest quotas were set in 2000 and 2001 when the population was at one of its lowest points (Laundré & Hernández, 2000), an estimated 16 resident animals of which 12 would be resident females (see calculations below). Thus, the legal quota, if filled by killing resident females, could take three quarters of the resident female population in this area. Such heavy reduction of matriarchal lines threatens both sustainability and the genetic diversity of puma populations (Loxterman, 2001).

The quotas in our Idaho study area were based on the erroneous notion that pumas were depressing deer herds and the demands by deer hunters to reduce this supposed threat. The Idaho legislature responded to this demand by appropriating $200,000 for predator control in 2000. Thus, even where we have reliable estimates of puma population size, local political considerations often override biological ones. In conclusion, we argue that none of these management approaches offers much security for the long-term survival of puma populations, yet they are variously institutionalized in state management programmes.

Developing a new management alternative

Since none of the present approaches to managing the hunting of pumas ensures their long-term survival, the question remains whether it is possible to achieve this goal under any system of hunting. If such a system is possible we believe that it must meet two major criteria: it must obviate the need for annual censuses of puma populations and it must provide some degree of buffering from the vagaries of political decisions that cause over-killing.

Appraising past management

Although none of the existing management strategies meets the desired goal, neither has their use up to this point, at least in the western states, led to the extinction of pumas. This may seem to contradict our original premise but can be explained by several factors. First, until the second half of the twentieth century, western states were very rural, with low population densities and poorly developed transportation systems. As a result, they retained relatively large areas with limited accessibility to hunters. Most control efforts before 1970 were concentrated in ranching areas. With the advent of hunting seasons on pumas, these remote areas experienced even less pressure. What resulted from all this was a system in which some subpopulations of pumas remained relatively secure from hunting while other, more accessible subpopulations received most of the hunting pressure.

We suggest that this system had the characteristics of a source-and-sink structure, as it is currently conceived in metapopulation biology (McCullough, 1996; Hanski, 1999). In this system, relatively large sources are able to supply new individuals to relatively small surrounding sink areas. Within the system, where large reservoir populations are surrounded by smaller sink populations, the harvest of pumas in the sink areas may have localized effects but does not endanger the long-term survival of the region's metapopulation. An example of such a system is the Frank Church River of No Return Wilderness area in central Idaho (Fig. 1). This relatively large area with limited access continues to produce high puma numbers (Hornocker, 1969; Seidensticker, *et al.* 1973). It thus supplies sufficient dispersing individuals to outlying sink areas, such as the Salmon-Challis area (Fig. 1), where, because of its accessibility, consistently high numbers of pumas (~71/year) are harvested (Idaho Fish and Game Department, 2001).

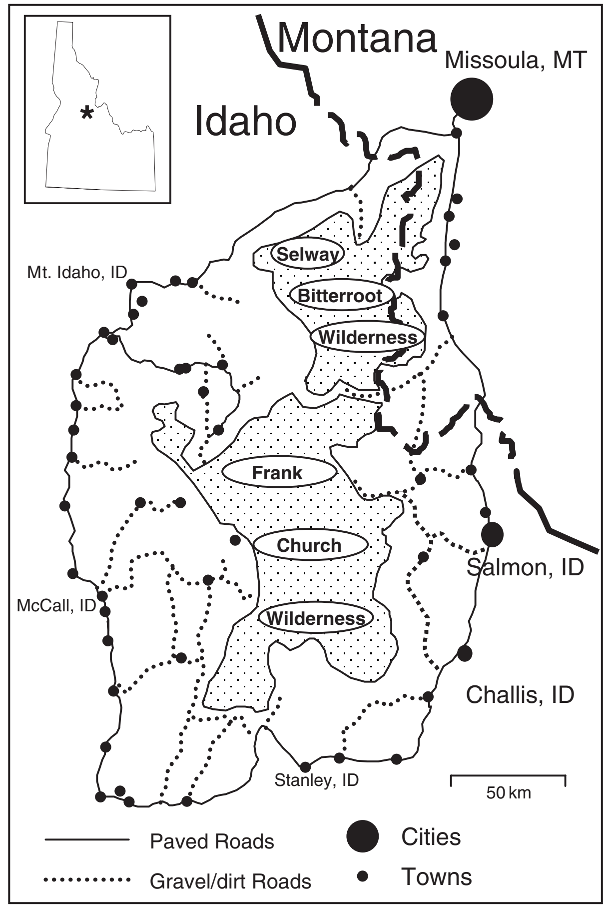

Fig. 1. Diagram of the Frank Church River of No Return Wilderness in Idaho where puma harvest is low because of accessibility. This area provides migrants to the surrounding areas where the harvest has consistently been high because of the high accessibility owing to the numerous roads and small towns in these areas.

What has happened in most areas in recent years, however, is an increase in puma hunters as well as in accessibility of formerly remote areas, resulting in smaller reservoir populations and larger sink populations. Such a system is unstable because the reservoir populations can no longer replace the losses of the sink areas and, because of the smaller population sizes, can no longer maintain viable populations. In such a situation, the maintenance of long-term viability would require accurate census data that are not attainable with current survey techniques (Choate *et al.*, 2000; Gratson *et al.*, 2000).

A new management proposal based on metapopulation structure

We propose a management plan that meets the goal of long-term survival of pumas based on metapopulation dynamics. In this plan some areas are designated as source areas (closed to hunting) and others are designated as sinks (open to hunting), in effect formalizing the system that existed in the past owing to limited access (Laundré *et al.*, 2000).

Critical to this plan is the assumption that pumas are mobile enough to function as a metapopulation. Our studies and others indicate that pumas are capable of dispersing more than 100 km over a variety of terrain (Ross & Jalkotzy, 1992; Beier, 1996; Laundré, 2000; Sweanor, Logan & Hornocker, 2000). Because of this, Sweanor *et al.* (2000) concluded that pumas in their New Mexico study area functioned in a metapopulation manner, and dispersal and genetic data from our study in southern Idaho and northwestern Utah also indicate a metapopulation structure (Fig. 2(a); Laundré, 2000; Loxterman, 2001).

Given that pumas can and probably do function on a metapopulation level, the goal is to maintain a viable population size within this metapopulation structure. To do this we need a physical area where pumas function in a metapopulation manner and that also has sufficient numbers of individuals to maintain a viable population. The size of such an area would be determined by available puma habitat and dispersal distances within the area. To determine the size of such an area, we suggest the use of the 'neighbourhood area', defined by Wright (1969) as the size of the area that contains the effective population size based on average dispersal distances and densities. Given the dispersal distances of pumas in an area, we can estimate the effective population size and the size of the elliptical neighbourhood area resulting from the formula of Wright (1969) as modified by Cavalli-Sforza & Bodmer (1971) for unequal dispersal directions: $N_e = \pi (2\sigma_x * 2\sigma_y)\ \delta$. The values σ_x and σ_y are the standard deviations of dispersal distances in two dimensions and δ is the density (number of resident animals/km^2). After calculating the neighbourhood effective population size, we removed density from the formula to estimate the size (km^2) of the elliptical-shaped neighbourhood area that contained this population. If the effective population size is sufficiently large ($N_e > 500$, Franklin, 1980), then we can be assured of maintaining the viability of pumas in this area.

Effective population size and genetic neighbourhood

We initially calculated an effective population size based on the 11-year average of minimum-density estimates of resident animals in our 2400 km^2 study area. All resident animals were reproductively active so the number of resident animals was assumed to equal the effective population size (Sinclair *et al.*, 2001). In our study area, σ_x and σ_y were based on the distance and direction of 16 dispersing animals, four females and 12 males (Fig. 2(a)), and equalled 40.4 km and 120.1 km, respectively (Laundré, 2000). From these data, we estimated an elliptical neighbourhood area of 60,970 km^2. Based on our trapping efforts, harvest reports and other available information, the 11-year average minimum-density estimate was 0.77 resident pumas/100 km^2 (including valleys, J. W. Laundré unpubl. data). Our resulting effective population size is 470 resident, reproductively active animals (Sinclair *et al.*, 2001). Population viability analyses for various large carnivores, including pumas, indicate that an effective population size of ~500 in an area as large as this should ensure survival for >100 years (Beier, 1993; Foley, 1994; Ludwig, 1999; Kelly & Durant, 2000). Thus, at least for our study area, the criteria of a metapopulation structure and adequate viability of the effective population size seem to be met.

We found that resident puma densities varied widely over 11 years (Laundré & Hernández, 2000; Table 1), and thus the use of a mean may not represent viability over this range, especially at lower densities. Consequently, in this example we will use maximum and minimum densities of resident animals we found over that period. Our minimum density of resident pumas was 0.58 individuals/100 km^2 and the maximum density was 1.04 individuals/100 km^2. We used these 'crude densities' (Smallwood, 1997) based on the total area of the study area (2400 km^2) because dispersal directions and distance are influenced by characteristics of the landscape. Based on these data, we estimated a minimum effective population of 353 and a maximum of 634 resident individuals (J. W. Laundré, unpubl. data) in a neighbourhood area of 60,970 km^2.

If we assume that the neighbourhood area now becomes the size of our regional management area, we just need to juxtapose this elliptical area in real space and then calculate actual puma densities. This ellipse could be centred anywhere but, for this example, we centred the neighbourhood ellipse on our study area. Centring the ellipse thus, however, illustrates one of the problems of delineating such areas, especially in fragmented habitats. The boundary of the ellipse includes large areas known to be unusable by pumas, e.g. parts of the Great Salt Lake Valley to the south and the Snake River Plain to the north. We adjusted for this by circumscribing a polygon (Fig. 2(b)) that approximated the size (~61,000 km^2) of the neighborhood area ellipse but eliminated areas unsuitable for pumas. Within this 'modified neighbourhood' polygon we further defined usable habitat, based on over 1,000 telemetry locations of female and male adult pumas (J. W. Laundré, unpubl. data), as areas in mountain ranges ≥ 2000 m elevation. The resulting usable habitat within this polygon was approximately 29,500 km^2.

Because the amount of usable habitat varied spatially within the modified neighbourhood (Fig. 2(b)), we used density estimates based on usable habitat to estimate maximum and minimum resident pumas in the polygon. For our study area (830 km^2 usable habitat within 2400 km^2) we calculated a maximum of 3.0 individuals/100 km^2 and a minimum of 1.7/100 km^2. With a total amount of 29,500 km^2 usable habitat, we estimated a minimum of 502 and a maximum of 886 resident animals within the modified neighbourhood.

Based again on 11 years of data, we estimated a mean of 12.4% resident males in the total population, 39.8% resident females, 31.2% kittens and 16.6% transient individuals (J. W. Laundré, unpubl. data). Assuming that the effective population size represents 52.2% (resident males and

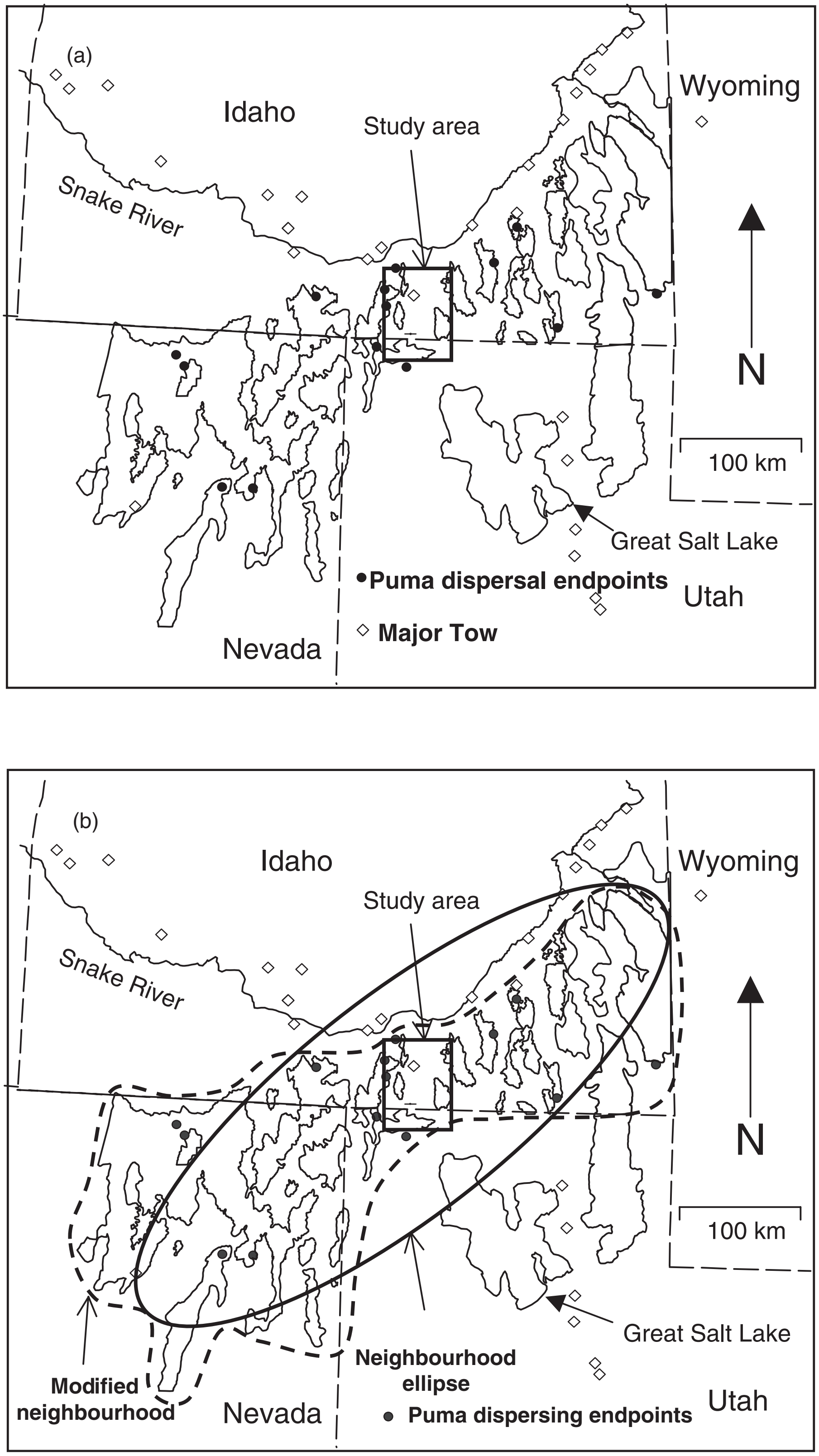

Fig. 2. (a) Sizes and locations of the various mountain ranges in southeastern Idaho, northwestern Utah, and northeastern Nevada. The location of the long-term puma study area is indicated. The endpoints of 14 of the 16 dispersing pumas used to estimate the neighbourhood area are indicated. Two animals dispersed more than 300 km, one to the northeast and the other to the southwest beyond the extent of the map. (2b) The size and shape of the estimated neighbourhood area ellipse centred on the long-term study area. The modified neighbourhood polygon represents the more biologically realistic positioning of an equal-size area relative to mountain range configurations in the region.

Table 1. Estimates of minimum densities (individuals/100 km^2) of resident pumas in the Idaho/Utah study area for 11 years. Estimates are based on total study-area size (2400 km^2) and on available puma habitat (830 km^2), defined as mountainous terrain ≥ 2000 m above sea level.

Year	Based on total study area	Based on available puma habitat
1991	0.77	2.05
1992	0.70	2.05
1993	0.66	1.93
1994	0.75	2.17
1995	0.95	2.77
1996	0.99	2.89
1997	1.04	3.01
1998	0.79	2.29
1999	0.66	1.93
2000	0.58	1.69
2001	0.66	1.93

females) of the total population, we thus estimated the total minimum population at 962 and the maximum at 1697 individuals. Of these totals, there would be a minimum of 119 and a maximum of 210 resident males, 383–675 resident females, 300–529 kittens and 160–282 transients.

Determining puma management units

Because pumas do not recognize political boundaries, we continued our regional analysis without recognizing the boundaries between Idaho, Utah, and Nevada. These numbers suggest that the neighbourhood area for our regional management area seems to include a sufficiently large number of resident animals, even at the low population estimate of 502, for long-term survival based on current criteria. This, however, does not consider removal of animals by hunting. Our goal was to find out if we can protect enough resident pumas to maintain viability within the context of removal. To do this we first needed to determine traditional harvest levels in this area. As all legal harvests need to be reported, we were able to use published harvest records. We used pre-1995 levels for Idaho because harvest levels since then have been driven more by political considerations than by biological ones and may not be sustainable. Harvest levels from 1975 through 1994 in southeastern Idaho averaged 31 animals/year (Idaho Fish and Game Department, 2001). In the Utah portion of the management area the harvest level from 1986 through 2000 averaged five animals/year, and in Nevada was approximately 30. Thus, historically, about 60–65 animals were removed per year from this area.

The goal of our proposed management plan is to create a system of sources (non-hunted areas) and sinks (hunted areas) that, first, ensures that we are protecting a viable population of pumas even at historically low densities and, second, still maintains traditional harvest levels. The closed or source areas in this system must be sufficiently large and positioned so that dispersal from them can replace losses in the sink or hunted areas. This could be accomplished in a variety of ways; we describe one example based on population sizes. Later we will discuss social and political considerations that can be used in final determination of the configuration of sources and sinks in any given area.

We first define 'sufficiently large' area. Our study area contained five mountain ranges that varied from 65 to 760 km^2 (Fig. 2(a)). The two smallest, the Cotterel (65 km^2) and Jim Sage Ranges (97 km^2), usually had only one to three resident females, and resident males usually included parts of nearby ranges in their territories. Over the 11 years of our study, neither subpopulation was self-sustaining (i.e. female kittens did not replace their mothers). Rather, young females from nearby ranges usually immigrated into these ranges to fill vacancies. The Black Pine Range (202 km^2), next in size, has had over the length of our study a self-supporting population of three to four resident females, even with hunter removal. We concluded from these data that ranges <100 km^2 were too small to be self-sustaining and thus probably acted as natural sinks. However, ranges >100 km^2, if protected from hunting, could function at least as intermediate-term sources (> 30 years).

Next we estimated the approximate area of each mountain range (≥ 2000 m elevation) within the regional management unit (Table 2) by digitizing the 2000 m elevation contours from 1:250,000-scale topographic

Table 2. Estimated area and minimum and maximum number of pumas within mountain ranges ≥ 2000 m above sea level for the different ranges of the example management unit

Mountain range code	Size km^2	Minimum number of pumas	Maximum number of pumas
Open to hunting			
O1	1725	29	52
O2	278	5	8
O3	760	13	23
O4	445	8	13
O5	65	1	2
O6	94	2	3
O7	2300	39	69
O8	17	<1	<1
O9	471	8	14
O10	21	<1	1
O11	66	1	2
O12	462	8	15
O13	82	1	2
O14	38	<1	1
O15	96	2	3
O16	81	1	2
O17	1207	21	36
O18	55	1	2
O19	2400	41	73
O20	245	4	7
O21	89	2	3
Totals	11,045	188	331
Closed to hunting			
C1	576	10	17
C2	167	3	5
C3	103	2	3
C4	472	8	14
C5	174	3	5
C6	671	11	20
C7	1483	25	44
C8	3790	64	114
C9	9535	162	286
C10	902	15	27
C11	415	6	7
C12	202	3	6
Totals	18,490	314	555

maps. Based on our low- and high-density estimates of resident animals for usable habitat, we then estimated the numbers of resident animals in each range (Table 2).

We based the selection of open and closed areas on three criteria – size, accessibility and juxtaposition. Mountain ranges < 100 km^2 were biologically considered sinks because of the small number of resident individuals, so we decided that they should remain open to hunting. There were 11 of these ranges and at the high population estimate they would have 28 animals (22 residents and six transients) vulnerable to hunting in Nevada (4) and Idaho (24). At the lower estimate, there would be 14 resident animals vulnerable in Nevada and Idaho. All other ranges were considered large enough to maintain viable subpopulations in the short term, ≈ 50 years (Beier, 1993, 1996).

In considering accessibility, we looked for any areas that historically had low hunting pressure or were protected (e.g. national parks). Such areas could be considered historical source populations, if large enough, and protection of these ranges would formalize this situation. In this region the only area that has officially restricted access is the Jarbridge Wilderness Area (JWA) (266 km^2), with no motorized access (Fig. 3). Considering the JWA alone, we estimate that it will have five to eight resident pumas – too few to be considered viable over the long term. However, the JWA is surrounded by a series of mountains with usable habitat ≥ 2000 m; these constitute a complex of 11,686 km^2 with an estimated 234 to 362 resident animals. To provide a buffer around the JWA, we closed to hunting a major portion of the range (9535 km^2, including the JWA, C9 in Fig. 3). We treated this area as a core source where there should be from 162 to 286 resident pumas (Table 2) and which should be a large enough area for long-term persistence (Beier, 1993). Because this source area is so large, we left open to hunting three ranges to the south, east and northeast as well as the southwestern portion (2416 km^2) of the JWA complex (Fig. 3). The southeastern part of the JWA complex was closed, as was another range to the northeast because we found that they act as corridors for dispersal of animals from our study area and probably from the JWA complex to the surrounding mountain ranges.

The easternmost range (C8 in Fig. 3) in the management area is actually part of the much larger Greater Yellowstone Ecosystem (GYE). Because areas to the east of this range are outside the management area and, for this exercise, are assumed to be open to hunting, we decided to close range C8 to act as a large source population (3790 km^2, 64–114 resident animals; Table 2). For the remaining mountain ranges, we selected a combination of closed and open areas that would provide some connectivity, specifically no more than one range open to hunting between protected populations. The smallest of the closed ranges is the Black

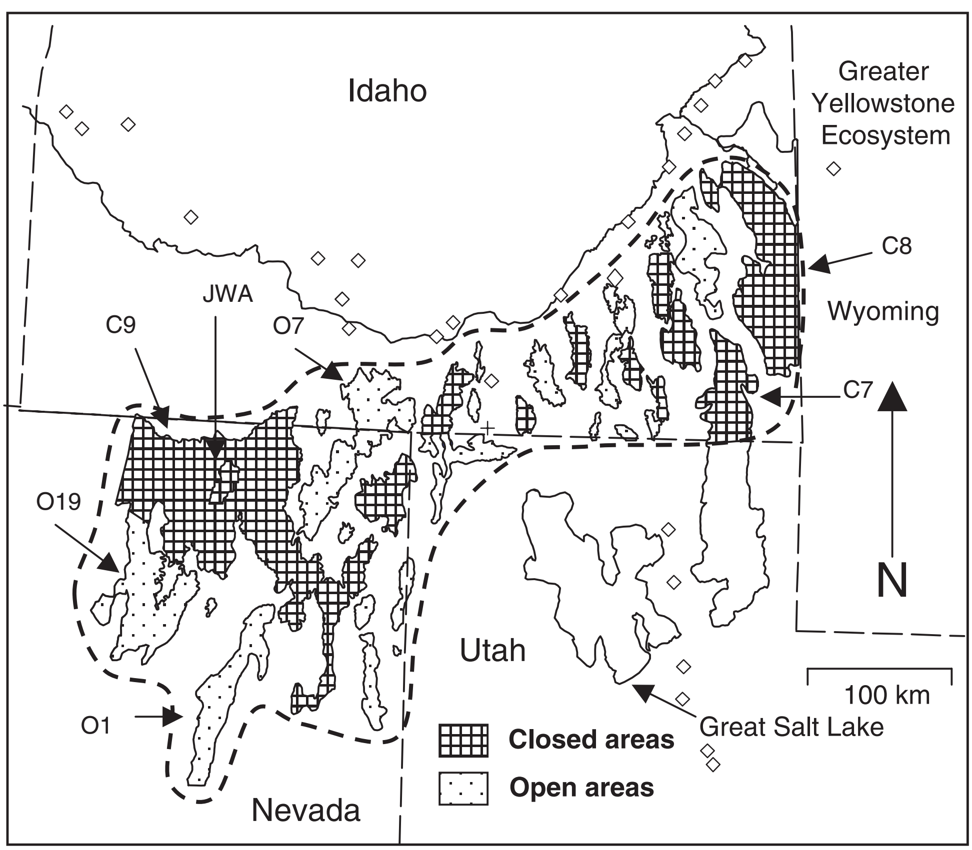

Fig. 3. An example of designating different mountain ranges within the modified neighbourhood area as either open (dotted) or closed (cross-hatched) to puma hunting. Some of the larger ranges listed in Table 2 are indicated. Table 2 lists the sizes of the various ranges and the corresponding number of ranges, the corresponding number of resident pumas estimated in each one.

Pine Range (202 km^2, four to six resident animals).

Within this configuration, we have approximately 18,600 km^2 of puma habitat with a minimum of 314 and a maximum of 555 resident individuals protected from hunting. This represents a total population of 602 to 1063 pumas with approximately 100 to 176 transients, primarily dispersing young, available to move to the open areas (Table 3). In the areas open to hunting, we have 187 to 331 resident animals and a total population of 358 to 634 pumas (Table 2). Of these, 246 to 436 (residents + transients) are susceptible to harvest (Table 3). If we assume an annual harvest rate of 60 animals, this represents 13.8 to 24.4% of the population.

With this sample configuration, we have demonstrated that, at higher puma densities, a sufficiently large population of resident animals (> 500) can be protected from hunting, while at the same time an adequate number of pumas is available for harvest at historical levels (~60–65). At the lower puma density (1.7/100 km^2 of usable habitat), only 314 animals are protected, fewer than the roughly 500 residents required for long-term survival. However, since only 60 animals would be harvested in the unprotected areas and if, in the worst case, they were all resident animals, it would still leave 149 resident animals in the huntable areas or 463 resident animals overall.

One factor to consider is the accuracy of the density estimates (1.7–3.0 individuals/100 km^2). Crude density estimates (Smallwood, 1997), based on total area studied and total number of animals detected (residents, juveniles and transients), averaged 4.0 individuals/100 km^2 and ranged from 0.30 to 13.03/100 km^2 (Anderson, 1983). We found two studies where crude densities of resident pumas were estimated. Spreadbury *et al.* (1996) estimated 0.9 residents/100 km^2 in British Columbia, and Ross & Jalkotzy (1992) estimated 2.2 residents/100 km^2 in Alberta. When we reconvert our high and low estimates of resident animals based only on usable habitat (mountainous areas ≥2000 m, or 29,530 km^2) to ones based on total area (~61,000 km^2), we come up with 0.82–1.45 individuals/100 km^2. Thus, the estimates from our 11-year study appear to be reasonable estimates of high and, especially, low densities for use in conducting this long-term large-scale analysis.

IMPLEMENTING THE MANAGEMENT PLAN

This exercise has demonstrated that by setting aside approximately 63% of puma habitat (Table 2), long-term viability of the Idaho/Utah/Nevada regional population could be maintained while also providing sufficient harvesting opportunities in the remaining unprotected areas. Variations on our approach are possible, given diverse contexts over the range of pumas in the west. However, several points need to be stressed.

Table 3. Summary of total area size and puma numbers in different sex and age categories in the areas open and closed to hunting

		Pumas			
Area status	Total area km^2	Resident males	Resident females	Transients	Kittens
Closed areas	18,590	75–132	239–423	101–76	187–332
Open areas	11,000	45–79	142–252	59–105	112–98

Some key considerations

First, the underlying premise of this management design is that the pumas in the designated region behave in a metapopulation manner. It is critical to the overall functioning of the system that young pumas are able to disperse from the designated source (closed) areas to the designated sink (open) areas. Based on our dispersal data, this currently seems to be a reasonable assumption. However, any disruption in the dispersal ability of pumas could have a major impact on the system on both population and genetic levels (Beier, 1993; Loxterman, 2001; Sinclair *et al.*, 2001). Thus, it is vital that once a regional management area is designated based on dispersal patterns, existing links or movement corridors among the various metapopulations must be maintained or enhanced (Beier, 1993).

Second, the amount and configuration of open and closed areas designated in this exercise were based primarily on biological criteria generated from our long-term study in the region. We stress that there could be a variety of other configurations that might also achieve the same management goal, depending on the situation and what people value. For example, we focused on individual mountain ranges or parts of ranges as units for designation. In reality there exists in the three states a system of hunting management units, originally established to manage deer hunting, that are currently used to designate seasons and limits to puma harvest. In some cases the boundaries of these units coincide with areas we designated in our example, and in fact, from an administrative point of view, mountain ranges or parts of ranges could be designated as open or closed to hunting based on these existing management units.

Third, we again emphasize that the delineation of the regional management unit (the modified neighbourhood polygon) was somewhat arbitrary. However, our polygon did include what could be considered a reasonable regional area to manage as a unit; that is, pumas regularly dispersed across this area, which is bounded on the north and south-southwest by large expanses of non-puma habitat. Although including lands under the jurisdiction of three states could complicate management, the biological data support such regional, multi-state approaches (Sinclair *et al.*, 2001).

Finally, another important point is that areas closed to harvest could still be open to pursuit only or catch-and-release puma hunting which is probably more common than hunting specifically to harvest an animal (Utah Division of Wildlife Resources, 1999). Although there is evidence that chasing and treeing pumas does cause stress (Harlow *et al.*, 1992), modest levels of such hunting in designated closed areas probably would not endanger resident animals. In over 14 years of fieldwork in our study area, we know of no incident where an adult animal was accidentally killed and only three incidents where kittens were killed by dogs. What constitutes ‘reasonable’ levels of catch-and-release hunting would have to be agreed on by diverse participants interested in puma conservation.

The implementation process

To accommodate various interest groups and stakeholders that probably have divergent perspectives on permitting puma hunting in particular areas we suggest a multi-stage process. First is for the game agencies, working closely with the public, to determine what areas might already be acting as reservoir populations by default and would probably continue to function as such. This could include designated wilderness areas, national parks and monuments, and inaccessible areas. The degree of protection in each area can be determined by analyzing current puma-hunting patterns, i.e. level of harvest/number of hunters. This will be easiest in states where there are regulated seasons, and hunters must check-in the animals they have killed along with information about where they hunted. In Texas, where approximately 98% of the land is privately owned (McGeveran, 2002) and the landowner determines hunting levels, a simple survey, asking how many animals are killed each year, would yield an estimate of how many subpopulations are currently afforded some protection. Population densities for each area can be derived either from field efforts or (at least initially) from estimates based on current literature. The sum of these estimates will give managers and interest groups a baseline estimate of how many pumas are currently protected, and the cooperative plotting of these locations on a map, as in our example, will show the proximity of these areas and allow estimates of puma numbers protected on a regional basis.

The next step is identifying gaps in the system – population gaps (where insufficient numbers of pumas are protected) or area gaps (where the configuration of subpopulations is inadequate to allow the metapopulation dynamics to operate). In many areas, such as central Idaho, sufficient puma numbers and adequate configurations of protected areas already exist. These areas will be the easiest to resolve; the management of puma hunting will only require formalizing what already exists. Some areas will require minimal modifications, such as closing some units to provide corridors for the metapopulation dynamics to operate or to boost subpopulations in reservoir areas. Surprisingly, such decisions may be easiest in Texas, where control over puma hunting lies with a relatively small number of private landowners. The metapopulation dynamics and the source and sink structure can be explained to them, and they can be offered incentives or otherwise encouraged to maintain a certain status, open or closed, for puma hunting. For other areas where decisions will need to be made regarding which areas should be closed and which should be open, more conflictual social and political factors will come into play.

Avoiding difficulties in joint decision making

It has been clear in Idaho (as mentioned earlier) and in many other states that the management of puma hunting has been decided in the past not only on biological information but also on interest-group politics. Although the states have jurisdiction over hunting and wildlife management, they are often pressured by many other interest groups and stakeholders who want to achieve their own ends. To complicate things, the states have interests of their own that they need to maximize. People generally organize themselves in an attempt to reach some kind of consensus on goals and plans, but, typically, the decision-making process involves diverse participants with conflicting perspectives and demands and with different strategies (persuasive or coercive) to achieve the outcomes they want (Clark, 2002). This process is vulnerable to less noble human traits such as aggressiveness, dogmatism, bureaucracy, and domination by special interests – including those of various segments of the public, ‘experts,’ and the agencies themselves (Clark & Brunner, 1996). The focus of participatory efforts, whatever shape they take, should be on collective problem solving. Community-based approaches are becoming popular, but they must be well organized and participants must be committed to improving the rationality of the process and finding common interest solutions rather than vying to control the outcomes to achieve their special interests (Clark & Gillesberg, 2001; Primm, 2001). Many authors have described community-based problem solving, its pitfalls and benefits, and offered practical designs (e.g. Wondolleck & Yaffee, 2000).

Officials and staff members in state management agencies, in cooperation with the public, must overcome both anticipated and unintended problems in their interactions. In some cases they must change the way they view and interact with the public, abandoning tendencies towards control, dismissing or limiting public input, or ‘domain defense’. An organization that can anticipate and address environmental trends, especially public attitudes, is in a much better situation to exercise control of its own destiny than one that waits until its domain is threatened. Adaptive negotiation and effective citizen participation can be beneficial. In all cases, the agencies need to work with the public towards integrated solutions in managing puma hunting in the west, leading to new perspectives and practices.

Despite the messiness of policy-making processes, there are standards by which to judge the success of such efforts, and all participants must strive to meet these (see Clark *et al.*, 2001: 43–4). Everyone should strive to acknowledge their own biases and make an effort to minimize them. All parties must commit themselves to clarifying and serving common interests and not allowing special interests, no matter how powerful, to subvert the process. Decision making should be inclusive, engaging everyone who might be affected by the outcomes, anyone who is interested and anyone who has something to contribute, and all interactions should be conducted with mutual respect. Decisions and actions should be timely;

delays usually exacerbate problems. Professionalism and personal diplomacy will be needed to bridge the hostility, resentment and ill will generated by past processes. In addition, joint problem-solving efforts must be based on factual, reliable information from credible sources. They must be fair and equitable to all parties. They should be ameliorative, not creating harm or disadvantage for anyone. They should be comprehensive and integrated; proposals and justifications must be complete so that people can assess them accurately.

Manfredo *et al.* (1998) and Riley & Decker (2000*a*,*b*), for example, describe the dynamics of puma management in Colorado and Montana, respectively, focusing on measuring the public's 'acceptance capacity' for pumas. Recent events in western Wyoming concerning puma hunting also illustrate how difficult it is to meet these standards, given the management philosophy, interest and approach of the state agency and the diverse demands of a variety of interested non-governmental groups (see Simpson, 1999*a*; McCoy, 2001). A sampling of newspaper headlines tells the story: 'Wyoming Game and Fish may add lion hunts: critics say anecdotal evidence of cougar increases insufficient' (Simpson, 1999*b*), 'Lions should be subject to better management' (Blessley, 2000), 'Killing cornered cats makes elk hunt easier' (Suttle, 2000), 'Lion hunters display the courage of Pooh' (Turner, 2000), 'Lion hunt justified' (Holz, 2000), 'Lion-hunting opponents attack Game & Fish ad' (Huntington, 2001), 'Insular agency' (Rundquist, 2001), and 'Game and Fish ignores mountain lion science' (Mangelsen, 2001), and 'Game and Fish hears lion policy criticism' (Rayster, 2001). The end of controversy is not in sight in this case. Our approach offers a way out of this morass.

CONCLUSION

In response to growing controversy over the hunting of pumas, we have proposed a management plan that can meet the long-term goal of sustainability of puma populations while maintaining historical hunting levels. Our plan is a compromise of sorts. Management of puma hunting can be based on metapopulation concepts (Laundré *et al.*, 2000). Our system calls for the designation of regional population groupings based on the dispersal patterns of pumas and large enough to contain a viable population of resident animals. Within these regional groupings, sufficient protected source areas are designated to supply dispersing animals to hunted sink areas. Management units within the regional grouping are open or closed to hunting, based on size, accessibility and juxtaposition, to achieve the goal of long-term sustainability under historically normal population fluctuations. Logans & Sweanor (2001) proposed a similar plan in which large regional tracts of land are totally open or closed to puma hunting. Such a large-scale approach is biologically sound but faces many political and social challenges that our small-scale approach is likely to avoid.

According to policy scientists, good policies or programmes should meet three criteria: they must be rational or reasonable, they must be politically practical and they must be morally justifiable (Clark *et al.*, 2001; Clark, 2002). Although the mix of scientific knowledge about pumas, diverse and dynamic public interests, and deeply rooted agency management traditions produces a complex and controversial arena in which to create 'good' policies for managing puma hunting sustainably, we believe that our management scheme promotes this end. First, it is reasonable. Given reasonable minimum and maximum estimates of resident puma densities, sufficient numbers of subpopulations can be maintained free of hunting pressure, thus ensuring long-term survival of the regional metapopulation, regardless of the hunting pressure exerted in the open areas. Also, since the size of the area designated for protection is based on the historic minimum density of resident animals, it eliminates the need for annual estimates of puma densities. Second, it is practical. Since a viable population of resident pumas is always protected, there would be less concern about the impact of hunting on the regional population, thus reducing the number and intensity of conflicts among interest groups that currently afflict management of this species. Third, it is justifiable. It is a reliable means to achieve the goal sought by managers, conservationists and hunters – the long-term sustainability of puma populations.

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