

# Metapopulations and Wildlife Conservation



**Edited by Dale R. McCullough**

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## Brown/Grizzly Bear Metapopulations



*F. Lance Craighead and Ernest R. Vyse*

In this chapter we examine the genetic and demographic dynamics of brown bear (*Ursus arctos*) populations in light of current metapopulation theory. Interior and arctic brown bears are often referred to as grizzly bears (Figure 14.1). Our research has centered on demographic and genetic studies of one such arctic brown/grizzly bear population. The characteristics of this population are typical of most historic brown bear populations: the bears occupy continuous habitat with frequent dispersal of individuals (usually males) between demes of more sedentary females. Brown bears are omnivorous, intelligent, and highly adaptable and can also be found in geographic situations that approximate classic metapopulation structures. Moreover, as large areas of occupied habitat have become fragmented due to human development, the "typical" structure has been replaced with smaller, isolated populations that may or may not interact as a metapopulation.

We begin by considering possible natural metapopulations within island systems and reviewing current mitochondrial DNA (mtDNA) and behavioral data. We then consider populations in continuous, mainland habitat, using our microsatellite DNA analyses and those of D. Paetkau and C. Strobeck, and discuss whether these systems can properly be termed metapopulations. We conclude by looking at habitat islands that have been fragmented by human activity and considering their metapopulation characteristics.

Brown bears may have evolved in Asia, most likely in forested habitat, or a tundra/forest mosaic. They dispersed throughout similar habitat, crossing the Bering land bridge into the New World about 35,000 (Talbot and Shields in press) to 40,000 years before the present (P. Matheus, University of Alaska, personal communication, 1995) or even earlier (Churcher and Morgan



Figure 14.1. Subadult grizzly bears on the tundra, Brooks Range, Alaska. Photo by H. V. Reynolds.

1976). Mitochondrial DNA sequence-divergence data (Waits et al. 1996a, 1996b; Talbot and Shields in press), when viewed in the light of fossil and molecular dating, indicate that there were at least two brown bear migration episodes from the Old World to the New World. These resulted in separate mtDNA lineages (or clades) in the New World. At the limits of their ancestral habitat, brown bears have adapted to new habitat types.

Brown bear populations probably reached the greatest extent of dispersal around the 1500s, before the widespread use of firearms. At that time there were two large continental populations in North America and Eurasia. The Eurasian distribution extended as far south as North Africa and the Middle East, while the North American distribution extended south into Mexico (Cowan 1972; Servheen 1990).

### Natural Island Metapopulations

During the last ice ages, as brown bear distribution reached the Russian Far East, populations were established on the Kamchatka peninsula and on the islands of Sakhalin, the Kuriles, and Hokkaido. These colonization events probably took place at about the same time as the first migrants colonized the New World, approximately 40,000 years before the present.

As they became established in Pleistocene Alaska, brown bears colonized the ABC Islands (Admiralty, Baranof, and Chichagof) in southeastern Alaska, the islands of Kodiak and Afognak, and the islands of Prince William Sound. Both mtDNA restriction fragment data (Cronin et al. 1991) and sequence data (Shields and Kocher 1991; Waits et al. 1996a, 1996b; Talbot and Shields in press) indicate that the ABC lineage is more closely related to polar

bears than are other brown bear lineages. This is probably the most ancient lineage in North America.

Very little is known about the population dynamics or the population genetics of brown bears on most of these islands. In the following section we speculate on likely metapopulation dynamics. As genetic data are collected and analyzed from these island populations, they should provide insights into the functioning of a wide variety of metapopulation structures. There appears to be a size limitation to islands that currently support self-sustaining bear populations. In many cases this limit appears to be related to the area necessary in a given climatic regime to develop salmon spawning streams large enough to provide a consistent food source. But area alone, without considering food availability, does not appear to be a good predictor of brown bear population size or, by extension, population persistence over time: there are several large islands adjacent to occupied bear habitat that do not support bears.

Few data are available on brown bear dispersal distances across water. Bears are powerful swimmers and have been observed many kilometers from land. A subadult brown bear released on an island in Prince William Sound swam perhaps as far as 15.1 km to return to his point of capture 93 km away within 28 days (Miller and Ballard 1982). Other anecdotal reports are discussed in the following sections. Although it appears that expanses of open water greater than about 5 km can act as a barrier (or a filter) blocking or restricting migration, such barriers are less effective against males, subadult males in particular. Of course, to create gene flow an individual must not only migrate but also successfully reproduce after crossing a barrier.

Many natural island metapopulations have been isolated to some degree and have persisted over long periods of time without the benefit of increased gene flow from neighboring or transient males. The population sizes and spatial structure of these metapopulations should provide some insight into the minimal configuration of areas and population sizes needed to maintain populations in human-fragmented habitat.

### *Sakhalin, Hokkaido, and the Kuriles*

Sakhalin and Hokkaido were connected to mainland Asia several times during the Pliocene and Pleistocene as sea levels varied (Figure 14.2). It is likely that both these islands were colonized around the same time. Because of their large numbers, it is unlikely that brown bear populations have ever gone extinct on either island. Sakhalin, with an estimated population of 1400 (Servheen 1990) in a 77,000-km<sup>2</sup> area, is less than 10 km from the mainland of the Russian Far East at the closest point and migrant individuals are probably exchanged occasionally. Hokkaido, about 40 km from Sakhalin, is more isolated and may have received no immigrants since the



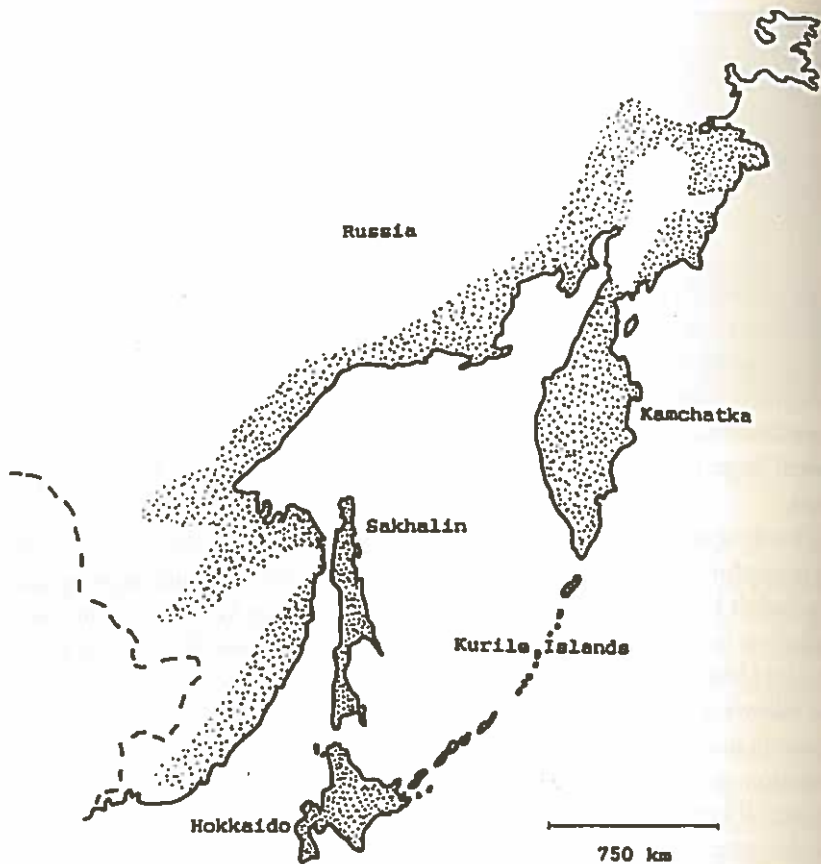


Figure 14.2. Map of Sakhalin, Hokkaido, and the Kurile Islands showing historic brown bear distribution. Stippled areas depict densities greater than 70 bears per 1000 km<sup>2</sup>. After M. Kretchmar, Institute of Biological Problems of the North, Magadan, Russia (personal communication).

last, Wisconsin, glaciation. Historically, however, Hokkaido may have supported as many brown bears as Sakhalin. Up to 3000 bears have been reported in recent times (Domico 1988), but Servheen (1990) considered the population size as unknown in 1989. The population is much reduced from historic levels due to increasing human alteration of habitat, and it appears to be fragmented into three subpopulations by human development (Servheen 1990). Hunting of brown bears on Hokkaido is currently allowed. The Asiatic black bear (*Ursus thibetanus*) is found on Hokkaido and on Honshu, Kyushu, and Shikoku islands farther south in Japan (Hanai 1985), so it is possible that the brown bear also used to occur farther south but has been extirpated.

Between Hokkaido and the Kamchatka peninsula the Kurile Islands form a classic stepping-stone array of smaller intermediate islands. Both Kamchatka, with 12,000 to 14,000 brown bears (Dunishenko 1987) in a 472,000-km<sup>2</sup> area (Revenko 1996), and Hokkaido have historically had large brown bear populations. Recent legal and illegal hunting abetted by the struggling Russian economy and the demand for bear gallbladders has markedly reduced the Kamchatka brown bear population (Revenko 1996). The larger Kurile Islands adjacent to either of these "mainlands" have resident bear populations that may periodically go extinct and then become recolonized. These larger islands are separated from each other and from the "mainlands" by about 25 km. A total of 700 brown bears is estimated on the larger Kurile Islands (Dunishenko 1987). Current bear populations are probably restricted to islands that are large enough to support salmon populations that spawn in freshwater streams (Y. Zhuravlev, Russian Academy of Science, Vladivostok, personal communication, 1994). The smaller islands in the center of the chain do not support resident bear populations.

Although it is possible that bears visit the nearer of these small islands, it is unlikely that migrant bears would travel the length of the chain. During glacial episodes, however, when these islands were larger and less distant, or connected as a peninsula, brown bears from Kamchatka could well have reached Hokkaido. There is a slight possibility of exchange in recent times between Sakhalin and Hokkaido. Recent research using minisatellite DNA fingerprinting of brown bears on Hokkaido reveals little genetic diversity (Tsurgu et al. 1994a, 1994b), but the interpretation of these results is difficult because, using a variety of minisatellite markers, grizzly bears exhibit very little variability (Craighead 1994). Additional genetic studies of these islands should reveal an interesting history and the current dynamics of this metapopulation.

### *Kodiak and Afognak*

Kodiak and Afognak islands both support viable brown bear populations and are near enough that there is a frequent exchange of individuals between them and between Raspberry Island, Shuyak Island, and other islands in the archipelago (Figure 14.3). Population density was estimated at about 208 bears per 1000 km<sup>2</sup>, or 2732 brown bears (1968–3538) in 13,191 km<sup>2</sup> (ADFG 1993). Excluding Afognak and Shuyak islands (with very different habitats), there are 2584 brown bears estimated in 9934 km<sup>2</sup>, or a density of 380 bears per 1000 km<sup>2</sup> (Barnes and Smith 1996). The archipelago was probably colonized during one or more glacial episodes when the islands were connected with the mainland Alaska peninsula or separated by a narrow barrier of water. These bears are sufficiently distinct morphologically to be considered the only current subspecies of brown bear, *Ursus arctos middendorffi*.



In recent times there have been occasional incidental sightings of brown bears swimming in the waters of Shelikof Strait between Kodiak and the Alaska peninsula, a distance of about 45 km. A mtDNA haplotype found in all Kodiak bears (Cronin et al. 1991) is also found among bears on the Alaska peninsula mainland. Moreover, mtDNA sequence data (Talbot and Shields 1995) indicate that there are distinct lineages on Kodiak and other distinct lineages in nearby Katmai on the Alaska peninsula. Additional sequences that are shared by both populations are also found throughout western Alaska and probably represent older lineages. There is thus some evidence for migration across Shelikof Strait: Kodiak may have been colonized from the Alaska peninsula mainland, or there may have been more recent interchange between Kodiak and the mainland. The emerging genetic picture indicates that there may be some gene flow provided by females (mtDNA) between Kodiak and the mainland. Given the greater dispersal of males, genetic interchange via males should be greater than that of females; this possibility is currently under investigation. The narrow straits separating Kodiak, Afognak, and other islands in the archipelago are not an effective barrier to gene flow by either sex.

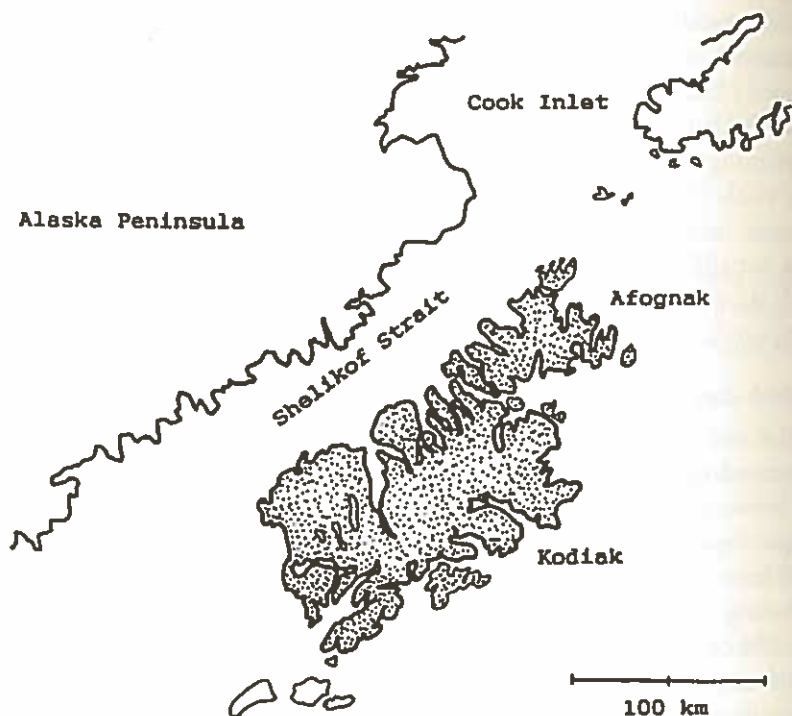


Figure 14.3. Map of the Kodiak Archipelago showing habitat permanently occupied by *Ursus arctos middendorffi* (stippled area). After ADFG (1993).

Unimak Island, adjacent to the Alaska peninsula in the Aleutian chain, is estimated to support 250 (200–300) brown bears (ADFG 1993). This population is almost certainly maintained by immigration from the mainland, which is less than 3 km distant. Resident populations are not found on the other Aleutian islands.

#### *Prince William Sound: Montague and Hinchinbrook Islands*

Both Montague and Hinchinbrook support brown bear populations (Figure 14.4). Population estimates are 55 to 139 for Hinchinbrook, 23 to 58 for Montague, 10 to 19 for Hawkins Island, and 11 to 22 for the Kenai Peninsula mainland adjoining western Prince William Sound (Nowlin 1993). No brown bears are considered resident on the islands of western Prince William Sound. Brown bears, as noted, can swim between these islands (Miller and Ballard 1982). It is likely that there is gene flow between Montague and Hinchinbrook, which are about 13 km apart, and it is more likely that migration takes place between Hinchinbrook, Hawkins Island, and the Alaskan mainland near Cordova, which are separated by less than 3 km. With only about 40 resident bears, Montague may occasionally be “rescued” by immigrants crossing the islands to the west from the Kenai Peninsula (less than 10 km apart) or migrating from Hinchinbrook to the east. Kayak Island, less than 3 km off Cape Suckling in the Gulf of Alaska, is estimated to have 3 to 10 brown bears (ADFG 1993).

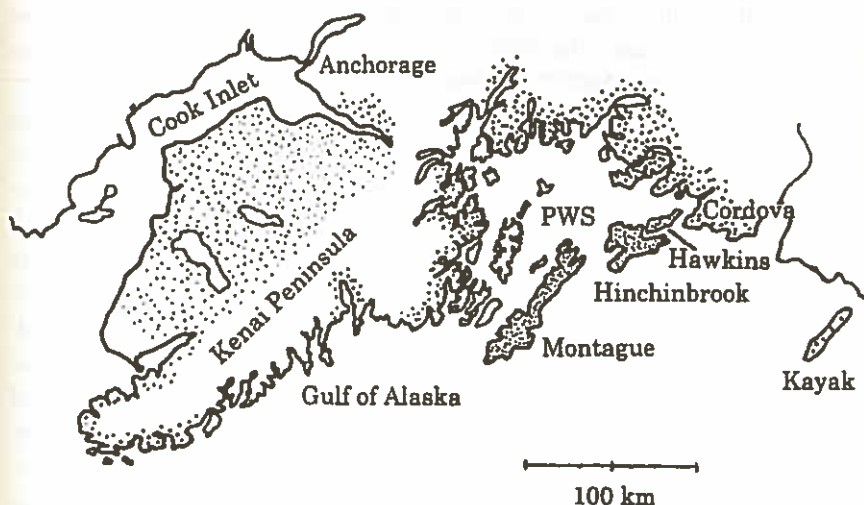


Figure 14.4. Map of Prince William Sound and the Kenai Peninsula showing habitat permanently occupied by brown bears (stippled area). After ADFG (1993).

### *The Kenai Peninsula*

The Kenai Peninsula in south-central Alaska supports an islandlike population of brown bears (Figure 14.4). It is connected by land to the rest of Alaska by a narrow corridor that is heavily glaciated. Gene flow through this corridor is no doubt greatly restricted. Estimates of population size are around 300 bears, with about 181 (90–270) in the western portion of the peninsula, 96 (50–150) on the eastern edge of the peninsula bordering the Gulf of Alaska and further north (ADFG 1993), and an additional 11 to 22 bordering Prince William Sound (Nowlin 1993). Gene flow probably occurs also into the Kenai through the coast and islands of Prince William Sound. Human population growth and development are proceeding rapidly on the Kenai, and salmon streams are crowded with anglers during salmon runs. Thus the population is probably reduced from historic levels.

### *The ABC Islands*

Admiralty, Baranof, and Chichagof islands (Figure 14.5) support brown bears at high population densities (ADFG 1993). Admiralty has an area of about 4306 km<sup>2</sup> and an estimated 1660 bears (1494–1824): a density of 386 bears per 1000 km<sup>2</sup>. Baranof covers about 4159 km<sup>2</sup> and has about 816 brown bears (719–913): a density of 196 bears per 1000 km<sup>2</sup>. Chichagof has an area of 5445 km<sup>2</sup> and an estimated 1625 brown bears (1501–1772): a density of 298 bears per 1000 km<sup>2</sup>. Kruzof Island has an area of 518 km<sup>2</sup> and supports an estimated 127 brown bears (121–133): a density of 245 bears per 1000 km<sup>2</sup> (ADFG 1993). Each of the larger islands may support viable populations, and each probably functions as its own “mainland,” although there is sufficient interchange that they share the same mtDNA lineages (Waits et al. 1996a; Talbot and Shields in press).

It is unlikely that Kruzof has a self-sustaining population; its numbers are probably augmented regularly by immigration from Chichagof over distances of less than 1 km between intermediate islands. It is unlikely that bear populations have gone extinct on any of the main islands since they were first colonized. This island group contains a large number of smaller islands that are presently separated by narrow expanses of water. Brown bears visit these islands and may remain on them for one or more generations, but the islands are not large enough to support a population over time. There are frequent anecdotal reports of bears swimming between Baranof and Chichagof (E. Young, Alaska Department of Fish and Game, personal communication, 1994), and a brown bear was observed 8 km from shore in Chatham Strait where Admiralty and Baranof are separated by 22 km of water (J. Faro, Alaska Department of Fish and Game, personal communication, 1994). Another bear was observed swimming in Freshwater Bay over 3 km from shore by

Titus and Beier (1992), who commented that expanses of water may not be barriers to some bears, especially subadult males. No radio-tagged animals have crossed from the ABC Islands to the mainland (K. Titus, Alaska Department of Fish and Game, as quoted by Talbot and Shields in press).

On the basis of distance alone, there should be significant gene flow between Baranof and Chichagof, which are 2 to 4 km apart in many places. Gene flow between them and Admiralty, about 8 km distant at the closest points, may be somewhat reduced. Recent mtDNA sequence data (Talbot and Shields in press) demonstrate a unique lineage on the ABC Islands that is not found on mainland southeastern Alaska. In addition, none of the mainland types that have been resolved to date are found in ABC brown bears either. Thus, it appears that there is little dispersal of female brown bears between the ABC Islands and the mainland, which can be as close as 4 or 6 km in places. Genetic and fossil data indicate that this is the most ancient lineage

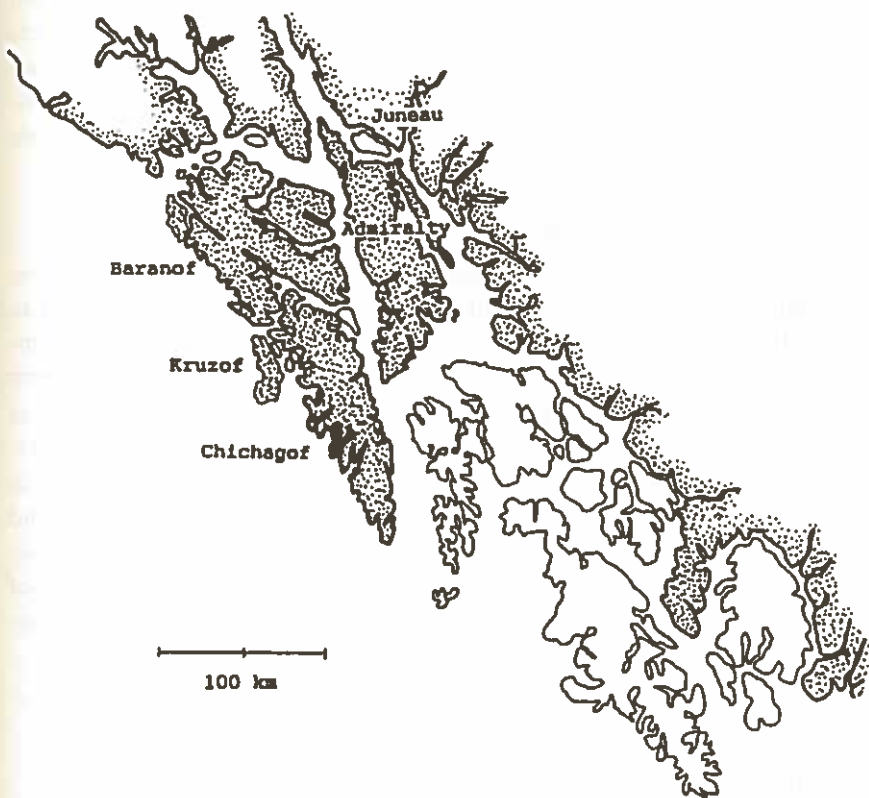


Figure 14.5. Map of the ABC Islands (Admiralty, Baranof, and Chichagof) showing habitat permanently occupied by brown bears (stippled area). After ADFG (1993).

of brown bears in North America and suggest, moreover, that they may have survived in a northwestern coastal refugium during the Pleistocene (Talbot and Shields in press). Further data from both mtDNA and nuclear genes will be necessary to clarify whether males occasionally cross these waters at the present time. In recent times, due to hunting pressure and widespread habitat modification caused by logging and other development, the populations on all three islands have declined but they are considered stable (ADFG 1993).

### *Richards Island*

Richards Island, on the MacKenzie River delta in Arctic Canada, supports a density of about four bears per 1000 km<sup>2</sup> (Nagy et al. 1983). It is adjacent to a large mainland population, less than 5 km distant, which ranges throughout the islands of the delta. A 17,318-km<sup>2</sup> area on the Tuktoyuktuk peninsula and Richards Island supports about 80 bears. Migration between these islands and the mainland is frequent enough that they should be considered a single population. There may be genetic differences between distant areas, but it is not likely to function as a metapopulation. This system is mentioned as an example of an island situation that probably does not act as a barrier to gene flow, as contrasted with Sakhalin and Hokkaido, or the ABC Islands, where genetic differences between island and mainland populations should be more pronounced.

### *Are These Metapopulations?*

None of the island systems discussed here appears to function as a classic metapopulation (Levins 1969; Gilpin 1987). Each system is connected to some degree to a "mainland" source of colonizing individuals. These mainlands may be large islands (Table 14.1) or continents that support brown bear populations in excess of 1000 individuals and tend to stabilize any true metapopulation dynamics. Nevertheless, the geographic separation affects the system dynamics and these island systems probably function as metapopulations in terms of population genetics (Paetkau et al. 1995) and also in terms of the spatial distribution of individuals (Hassel et al. 1994). With these caveats in mind, and given the more liberal definition of metapopulations exemplified by this volume, we will call these island systems metapopulations.

## **Continental Metapopulations**

Our discussion of continental populations is based primarily on intensive demographic and genetic studies of a population located in northwestern

TABLE 14.1.  
Isolated and semi-isolated island population estimates  
for various brown bear populations

Population	Estimated size	$N_{e1}$ <sup>†</sup>	$N_{e2}$ <sup>‡</sup>
Sakhalin Island	1400	420	574
Kurile Islands	700	210	287
Kodiak archipelago	2732	820	1120
Admiralty	1660	498	680
Baranof	816	245	335
Chichagof	1625	488	666
Kruzof	127	38	52
ABC Island archipelago	4228	1268	1733
Kenai Peninsula	300	90	123
Hinchinbrook	97	29	40
Montague	40	12	16
Northern Continental Divide Ecosystem	681	204	279
Yellowstone Grizzly Bear Ecosystem	236	71	97
Cabinet-Yaak Ecosystem	17	5	7
Selkirk Mountains Ecosystem	30	9	12
Western Brooks Range <sup>a</sup>	153	46	64
Tuktoyuktuk <sup>a</sup>	80	24	33

Note: In calculating  $N_e/N$ , note that  $N$  represents the total number of adults of breeding age in the population. In the field, this is usually difficult to determine accurately and total bears are estimated. Using estimates derived from our data, we determined  $N_e/N$  to be about 0.64 (Craighead 1994). When  $N$  is used to represent the total bear population (not just those of breeding age),  $N_e/N$  is about 0.41.

<sup>†</sup>  $N_{e1}$  = using Harris' (1986) estimate of  $N_e/N = 0.3$  and taking  $N$  to be the total population size.

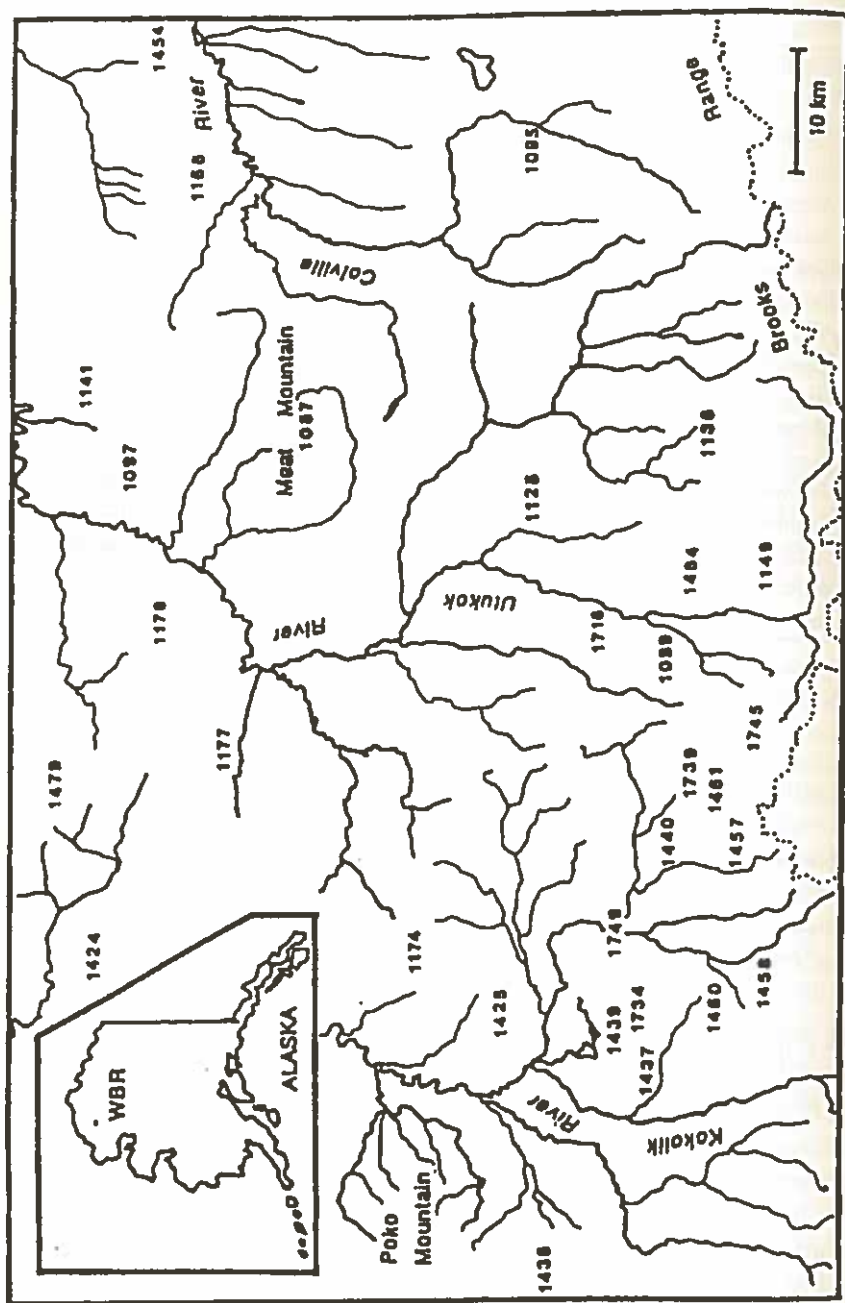
<sup>‡</sup>  $N_{e2}$  = using estimates from our data of  $N_e/N = 0.41$  when  $N$  represents the total population size.

<sup>a</sup> Nonisolated, contiguous arctic populations.

Alaska (Figure 14.6) in the northern foothills of the Western Brooks Range (WBR) around 69°N latitude, 161°W longitude. It encompasses the headwaters of the Colville, Utukok, and Kokolik rivers in an area of 5200 km<sup>2</sup>. Elevation ranges from 400 to 1300 m. The climate is dominated by long severe winters with short cool summers. This is near the northern limits of past and present brown bear range. It is open, treeless arctic tundra and is virtually undisturbed and unhunted. It has probably been inhabited by brown bears since they first arrived from Asia.

The bears inhabiting the area are part of a larger population of grizzly bears found throughout the DeLong Mountains of the Brooks Range. We





assume that the population dynamics and genetics of our study population are representative of most nearctic and palearctic brown bears existing in continuous habitat with no geographic barriers to dispersal. In fact, there are no geographic barriers to bear movement except the Arctic Ocean to the north and the Bering Strait to the west.

The state of knowledge of brown bear genetics is such that we will paint only a general picture of typical population genetics and dynamics based on our work with Paetkau and Strobeck (Paetkau and Strobeck 1994; Paetkau et al. 1995; Craighead et al. 1995). This picture is rapidly being defined, however, by work at the University of Alberta (Paetkau and Strobeck 1996) and the University of Utah (Waits et al. 1996a) in comparing grizzly populations across North America.

The WBR population has been studied continuously since 1977 by the Alaska Department of Fish and Game. During that time 256 individual bears have been captured. Particular emphasis was placed on radio-collaring adult females. Their offspring were subsequently radio-collared just before weaning whenever possible. Adult males were radio-collared whenever they were encountered or as time and available transmitters allowed. Monitoring of radio-collared animals has resulted in detailed knowledge of maternal/offspring relationships for 53 family groups (Reynolds 1978, 1980, 1989, 1991, 1992; Reynolds and Hechtel 1980, 1984). Whole blood or tissue samples were collected from all animals handled since 1986; 152 individuals were used for genetic analysis comprising 30 of the known family groups.

Total DNA was isolated from blood and tissue samples as described by Craighead (1994) and Craighead et al. (1995). Eight DNA microsatellite primer sets were developed by D. Paetkau (Paetkau and Strobeck 1994; Paetkau et al. 1995). These microsatellite loci were amplified using PCR and analyzed in an automatic DNA sequencer as detailed in Paetkau and Strobeck (1994) and Craighead (1994). The biological function of the alleles we examined is not known, but they segregate in a Mendelian fashion and appear to be selectively neutral. Each primer set amplified the two alleles at a single locus, for a total of 16 alleles per individual bear.

### *Pedigrees and Paternity*

Our study population was estimated in 1992 to consist of 153 bears in a 5200-km<sup>2</sup> area: a density of 29.4 bears per 1000 km<sup>2</sup> (H. Reynolds, Alaska Department of Fish and Game, personal communication). The 152 bears in our genetic sample included 75 males, 75 females, and 2 bears of unknown sex: 35 males and 45 females were of breeding age (5 years or older). The eight microsatellite primer sets amplified 61 unambiguous alleles in this population. We obtained complete genotypes at eight loci for all of these

individual bears (2432 alleles) (Craighead et al. 1995a). Mothers of 57 offspring were known. We were able to identify 12 fathers for 36; the remaining 21 were sired by at least 7 males that had not been sampled. No single male was responsible for more than 11 percent of known offspring, and no males younger than 9 years of age were successful. The fact that three paternal alleles were found at several loci is clear evidence that more than one male could contribute gametes to a litter. Multiple paternity was assigned, or deduced, in one-third of the known litters having two or more cubs (Craighead 1994; Craighead et al. 1995).

Examination of allele frequencies, occurrence of homozygotes, and occurrence of heterozygotes indicates that loci are in Hardy-Weinberg equilibrium. Allele frequency divergence between generations indicates that they are selectively neutral. Mutation or recombination rate was estimated at between 7.1 and  $2.2 \times 10^{-3}$  (Craighead 1994; Craighead et al. 1995).

### *Evidence of Population Structure*

Our observations and those of other researchers (Pearson 1975, 1977; Glenn 1980; Reynolds 1978; Nagy et al. 1983; Reynolds and Hechtel 1984; Knight et al. 1984; Miller 1984) demonstrate that female offspring tend to remain near their maternal home range after weaning and in some cases establish overlapping home ranges. Mothers and daughters often interact throughout their lives, occasionally foraging and raising young in close proximity to each other. Because adjacent females tend to be more closely related than distant ones, we might expect that genetic subdivision would occur over time; homozygotes would accumulate in local areas, and there would be a noticeable deficiency of heterozygotes (Wahlund effect) when the population is viewed as a panmictic unit.

We examined the data for evidence of a Wahlund effect at a local scale (following the definitions of Hanski and Gilpin 1991) within the study area. Within the WBR population, expected homozygosity (of genotype  $ii$ ) was calculated as  $p_i^2$  for each homozygote at each locus, where  $p_i$  is the frequency of the  $i$ th allele. Average expected heterozygosity ( $H$ ) was calculated as  $1 - \sum p_i^2$  and was 0.747 for the WBR sample. Measures of heterozygosity can differ greatly, depending on the molecular techniques used. Allozyme analysis (K. Knudsen, University of Montana, personal communication) and minisatellite probes (Craighead 1994) tend to give lower values of  $H$  than we obtained using microsatellite primers.

Observed  $H$  in our sample was calculated by enumerating all heterozygotes and homozygotes at each locus from the database. Differences between expected and observed  $H$  were examined using chi-square contingency analysis to determine if there was a deficiency of heterozygotes in the popula-

tion. We found no evidence of population subdivision in the WBR (Craighead 1994).

Because we know that females do not tend to migrate, the apparent panmixia at this scale seems to be due to the wide-ranging movements of the male segment of the population. This interpretation is supported by our paternity analysis: of 57 offspring whose mothers were known, only 36 were fathered by males for which we had genetic samples, despite the fact that we sampled males in the study area intensively over a 6-year period (Craighead et al. 1995a, 1995, 1996). Twenty-one of our known offspring were fathered by males that had not been captured and probably utilized the study area as only a part of their home range or passed through it as transients.

Long movements of male grizzlies are supported by radio-tracking data. Subadult males, in particular, often travel long distances (Glenn 1980; Craighead and Mitchell 1982; Reynolds and Hechtel 1984). One adult male, resident in our study area for several years, was later shot near Barrow, a distance of about 300 km (H. Reynolds, Alaska Department of Fish and Game, personal communication). Another adult male traveled 163 km to the Arctic Ocean coast and then returned (Reynolds and Hechtel 1984). Thus, individual males may occasionally travel hundreds of kilometers and then breed successfully.

With this spatial structure it is difficult to say where one metapopulation ends and another begins. Paetkau et al. (1995) have analyzed gene flow in polar bear metapopulations and found significant differences in allele frequencies between sample areas across the Canadian Arctic. If we use Hanski and Gilpin's (1991) definition of the metapopulation scale—"the scale at which individuals infrequently move from one place (population) to another, typically across habitat types which are not suitable for their feeding and breeding activities, and often with substantial risk of failing to locate another suitable habitat place in which to settle"—the differences in allele frequencies found between distant populations (Paetkau et al. 1995) indicate that a metapopulation structure does exist for polar bears on a large scale: on the order of several hundred kilometers.

A somewhat smaller scale applies to brown bear populations. An analysis of North American brown bear populations (Paetkau and Strobeck 1996) demonstrates a cline in allele frequencies throughout the occupied range. Genetic distance correlates closely with physical distance. Heterozygosity is reduced from about 70 percent in northwestern populations to 55 percent in the Yellowstone ecosystem. The Kodiak population, which is reproductively healthy, has 26 percent heterozygosity, however, so this does not indicate inbreeding depression (Paetkau and Strobeck 1996). Brown bears do not migrate over such great distances as polar bears; consequently, the

metapopulation scale for brown bears is expected to be somewhat smaller. Extinction and colonization events do not occur within local populations, but gene flow is restricted and areas of negative growth rate are probably "rescued" by adjacent areas with positive growth rates.

### *Size of Local "Populations"*

The local population unit in a continental metapopulation may conceivably be defined as the largest or the mean home range size, as the greatest or the mean dispersal distance, or perhaps as the genetic neighborhood size (Wright 1969). Wright defined neighborhood size with the equation

$$N_e = \pi \delta \sigma^2$$

where  $N_e$  = genetic effective size of the population

$\pi$  = 3.1416

$\delta$  = number of breeding adults per unit area

$\sigma^2$  = one-way variance of distance between birth and breeding sites

In our Western Brooks Range population we estimated values of  $N_e$  = 63.6 using Wright's (1931) original equation for unequal breeding sex ratio and  $N_e$  = 116 using Hill's (1972) equation, which incorporates variance in progeny number (Craighead 1994). Using the more conservative estimate of  $N_e$  = 63.6 and a density of 15.6 breeding adults (from a total of 29.4 bears) per 1000 km<sup>2</sup> (H. Reynolds, Alaska Department of Fish and Game, personal communication, 1993), we obtain a value of  $\sigma^2$  = 36 km. Accordingly, 99 percent of the individuals in a "population," by this rough estimate, have their offspring within a radius of  $3\sigma$ , or about 108 km (36,644 km<sup>2</sup>), around a given point.

An area this size in the Western Brooks Range would support about 570 effective breeding brown bears. There could be roughly five "populations" of this size in the arctic metapopulation between the Bering Strait and the MacKenzie delta. This is a much larger area than that occupied by our study population (which we know to be too small for genetic differentiation) and is also much larger than that of many of the island populations discussed earlier (Table 14.1). This implies that females in island populations have a more restricted pool of male gametes, since the genetic neighborhood is reduced by geographical barriers.

Accordingly, genetic variability is probably lower on isolated islands and on human-fragmented islands of habitat (varying with the length of time since isolation). Island and coastal habitats where salmon are present as a food source, however, maintain densities of brown bears that are about tenfold greater than areas of arctic or interior habitats (ADFG 1993; Servheen 1993).



The genetic neighborhood, or size of a "population," in these habitats will be correspondingly smaller than in the Arctic, since a population of 570 bears (or whatever the true genetic neighborhood encompasses) will be supported in a smaller area.

### **Are Continental Populations Metapopulations?**

Historically, brown bear populations expanded across Eurasia during the Pliocene/early Pleistocene and across North America during the late Pleistocene/early Holocene. Their ability to utilize a wide variety of habitat types would have resulted in a more or less continuously occupied area. Local populations have maintained relatively high levels of genetic diversity through gene flow resulting from the extensive movements of males, but allelic frequencies differ as distance increases (Paetkau and Strobeck 1996). This structure does not fit the classic metapopulation definitions of Levins (1969) or Gilpin (1987) but may function as a metapopulation in terms of population genetics (Paetkau et al. 1995; Paetkau and Strobeck 1996) or the spatial distribution of individuals (Hassel et al. 1994). Although this situation stretches the definition of a metapopulation, human activities are fragmenting the distribution of continental grizzly bear populations, and in an increasing number of areas bears are being reduced to a metapopulation.

### **Human-Fragmented Island Metapopulations**

Habitat fragmentation caused by development has been a major force around the world. In some cases it has reached a point where habitat patches have become isolated, and brown bears, to survive, must function as a metapopulation.

#### ***Europe***

Brown bears appear to have survived the Pleistocene glaciations in two refugia in Europe, resulting in two distinct mtDNA lineages (Kohn et al. 1995, 1996). Brown bears subsequently expanded throughout Europe and even inhabited the British Isles until the tenth century (Curry-Lindahl 1972; Servheen 1990). Since then, populations in Europe have been severely reduced and habitat has been fragmented by human modification (Figure 14.7). Viewed as a metapopulation, Europe has a large "mainland" population in northwestern Russia and Finland. Other smaller and more isolated populations exist throughout Europe (Table 14.2). Many of these populations in Western Europe are so isolated that they probably cannot function as





Figure 14.7. Map of brown bear distribution in Europe. Stippled areas depict known brown bear populations. After Servheen (1990).

TABLE 14.2.  
Estimated brown bear populations in Europe

Area	Estimated population	Source
Sweden and Norway	>700	Swenson (1994), Swenson et al. (1996)
Finland	450	Pullainen (1989)
Poland	70–75	Jakubiec and Buchalczyk (1987)
Slovakia and Czech Republic	700	Rosler (1989)
Southwestern Russia and Romania	6000	Rosler (1989)
Yugoslavia (1989)	1600–2000	Isakovic (1970), Huber (1992)
Bulgaria	850	Spiridonov and Spassov (1992)
Albania	Unknown	Servheen (1990)
Greece	90–170 <sup>a</sup>	Mertzanis (1989)
Italy	50, 10–16 <sup>b</sup>	Boscagli (1987), Zunino (1992)
Pyrenees Mountains	20–30	Camarra and Parde (1992)
Spain	93–103, 17 <sup>b</sup>	Clevenger et al. (1987)

<sup>a</sup> Total for two populations.

<sup>b</sup> Estimates for each of two populations.

a metapopulation, and some are likely to go extinct in the near future unless they are colonized by translocating bears from other areas. One Italian population is now estimated to contain only two or three bears based on DNA analysis of scat samples (Kohn et al. 1995, 1996). Brown bear populations are expanding in Sweden, however, where male bears have recolonized areas much more rapidly than females (Swenson et al. 1996). The brown bear populations in Eastern Europe—Romania, Greece, Albania, and southern Yugoslavia—occur in forested ecosystems separated by lowland areas of human development, and there is a possibility of a functioning metapopulation if linkages are maintained (Servheen et al. 1996). However, both legal and illegal hunting have increased in Russia, Romania, and Bulgaria since the collapse of the Soviet Union (C. Servheen, U.S. Fish and Wildlife Service, personal communication), and civil war in the former Yugoslavia has reduced bear numbers and further fragmented the habitat (Huber 1994).

### *Eurasia*

Brown bears are distributed throughout Eurasia (Figure 14.8) with a large "mainland" population in tundra and taiga forests of Russia extending into



Figure 14.8. Map of brown bear distribution in Eurasia. Stippled areas depict known brown bear populations. After Servheen (1990) and M. Kretchmar, Institute of Biological Problems of the North, Magadan, Russia (personal communication).

neighboring areas of North Korea, Mongolia, and China (Servheen 1990). The distribution and population sizes in these areas are not clearly known. Large areas supporting brown bears are found in central China and in Turkey, and there are smaller population "islands" along the China/Russian border and in parts of northern India, Pakistan, Iran, Iraq, Syria, and possibly Lebanon (Servheen 1990). Habitat in all these areas is declining, and there is little or no protection from hunting. There are barriers to dispersal, such as the Gobi Desert, and intensive human development in lowland areas so that it is not known whether some of these areas may function as a metapopulation.

### *North America*

Brown bear populations in the lower 48 states have also been greatly reduced in number, and their habitats have been fragmented by human development. The remnant populations form a potential metapopulation with three major large "islands" of bear habitat in the United States and adjacent Canada; these have been designated as the Northern Continental Divide Ecosystem (NCDE), Bitterroot Ecosystem (BE), and Yellowstone Grizzly Bear Ecosystem (YGBE) recovery zones by the U.S. Fish and Wildlife

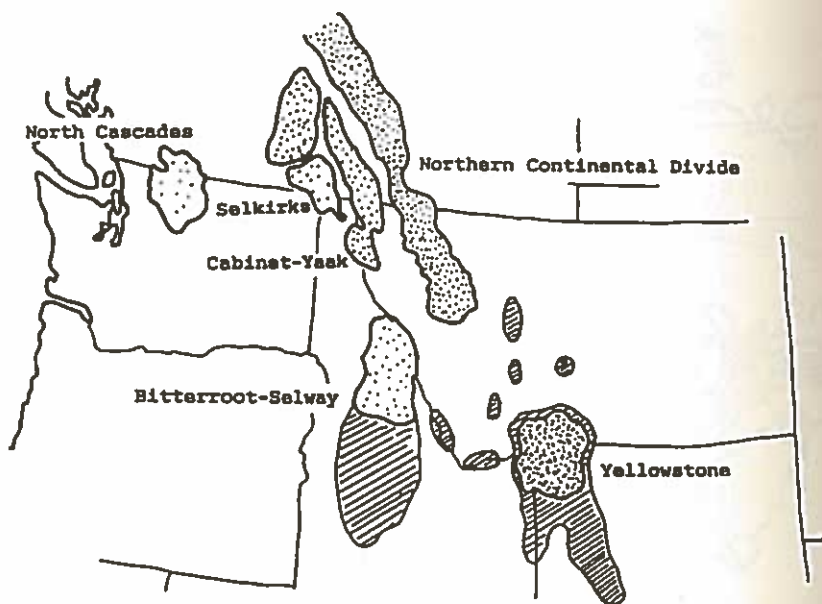


Figure 14.9. Map of brown bear habitat islands in North America. Stippled areas depict recovery zones; cross-hatched areas signify additional habitat. After Servheen (1990).

Service (Servheen 1993) (Figure 14.9). The cores of these areas are protected as national parks (in both the United States and Canada) and wilderness areas. Additional lands around these cores are at present undeveloped and contain brown bear habitat. Smaller islands of habitat exist, largely in Canada but extending over the U.S. border in the Cabinet-Yaak Ecosystem (CYE) and Selkirk Mountains Ecosystem (SE). A small and more isolated island of habitat is located in the North Cascades in Washington and British Columbia. These areas have also been designated as recovery zones. Areas of habitat designated as recovery zones have been calculated as sufficient to support a minimum brown bear population size (recovery goal) deemed large enough to be self-sustaining (Servheen 1993). Between the three large-land recovery zones there are small "stepping stones" of habitat that might be linked as corridors for movement if human development has not created impassable barriers. There is some evidence that bears occasionally move, or attempt to move, along these corridors (Picton 1986).

There is currently no clear consensus on brown bear numbers within the NCDE. Figures range from a Montana Department of Fish, Wildlife, and Parks estimate of 549 to 813 bears (a density of about 22.1 per 1000 km<sup>2</sup>) (Dood et. al. 1986) to a U.S. Fish and Wildlife Service estimate of a minimum 306 bears (87 adult females) (Servheen 1993), with a recovery goal of 591. At least 236 bears (67 adult females) are estimated for the YGBE, with a recovery target of 15 females with cubs per year (a density of about 11.2 bears per 1000 km<sup>2</sup>). Only 15 to 20 bears (a density of about 2.2 bears per 1000 km<sup>2</sup>) are estimated as a minimum population for the Cabinet-Yaak (within the United States), with a recovery goal of 106 for the area on both sides of the border. A minimum of 25 to 36 bears (a density of about 4.9 bears per 1000 km<sup>2</sup>) is estimated in the Selkirk Recovery Zone in both the United States and Canada, with a recovery goal of 90 bears on both sides of the border (Servheen 1993). Although the Bitterroot and North Cascades have historically supported brown bear populations, at present there are few, if any, bears residing in these areas.

### Can We Design a Metapopulation?

As noted earlier, self-sustaining populations of brown bears on islands or groups of islands have persisted perhaps for millennia. Island metapopulations known to have persisted in isolation have probably maintained populations in excess of 1000 brown bears. These island populations are contrasted with those of smaller islands in Table 14.1. Yet, smaller "islands" such as Animak (250), the Kenai Peninsula (300), Kruzof (127), Hinchinbrook (97),

Montague (40), and the Kurile Islands have also persisted for long periods of time adjacent to large "mainland" sources of immigrants.

The success of brown bears on island systems offers hope for the maintenance of a metapopulation of brown bears in the lower 48 states if functional routes for dispersal can be maintained between the core reserve areas. If such routes are closed by human activity, translocation may be required to maintain a functioning metapopulation structure.

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