Are black bears a factor in the restoration of North American grizzly bear populations?

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Abstract: We assess the potential for American black bears (*Ursus americanus*) to limit the growth of colonizing or severely reduced grizzly bear (*Ursus arctos*) populations. Managers are faced with the challenge of increasing the size of small ($N < 75$) grizzly bear populations in the North Cascade, Selkirk, Cabinet–Yaak, and Bitterroot recovery areas of the USA and Canada. These populations are mainly limited by human-caused mortality. However, other factors such as competition from black bears could impose additional constraints. Brown and grizzly bears and American black bears evolved separately until about 13,000 years ago and, as a probable consequence, they can have substantial diet overlap. Where meat and roots are available, grizzly bears consume more of these foods than do black bears. Where fleshy fruits and succulent forbs are the primary high quality bear foods, as in the North Cascade, Selkirk, and Cabinet–Yaak ecosystems, dietary overlap between grizzly and black bears can be almost complete. Largely because they are smaller, black bears can exist at roughly 10 times the density of grizzly bears, use ranges that are, on average, four-fifths smaller, and are more efficient than grizzly bears at using low densities of small berries. We postulate that the primary impact of black bears on grizzly bears is through reduced reproduction and recruitment caused by exploitation competition, despite the documented ability of most grizzly bears to dominate most black bears during physical confrontations. Such an effect would be greatest in areas where both species rely on berries and forbs, where grizzly bear populations have been extirpated, substantially reduced, or are absent but within dispersal distance, and where black bear populations are comparatively robust. On this basis we postulate that exploitation competition by resident black bears, together with mortality caused by Native Americans, slowed or even curbed the invasion of grizzly bears east across North America during the late Pleistocene and early Holocene. We also postulate that grizzly bears are absent on some coastal islands within dispersal distance of robust grizzly bear populations because of competitive exclusion by black bears.

Key words: American black bear, biogeography, brown bear, Cabinet–Yaak, competition, grizzly bear, North America, North Cascade, restoration, Selkirk, Selway–Bitterroot, *Ursus americanus*, *Ursus arctos*

There are several areas in North America where grizzly bears (*Ursus arctos*) survive as small, low-density populations, or where suitable habitat exists but grizzly bears have been extirpated. Fewer than 10–50 animals persist in an isolated population in the North Cascades of British Columbia (BC) and Washington state (Romain-Bondi et al. 2004), in a roughly 26,000-km^2 area that could support several hundred bears (North Cascades Grizzly Bear Recovery Team 2001). Small populations (<75 animals) also occur in the Selkirk region of BC, Washington, and Idaho, and in the Cabinet–Yaak region of BC, Idaho, and Montana (Fig. 1). Although not as isolated as conspecifics in the North Cascades, grizzly bears in the Selkirk and Cabinet–Yaak regions are partially hedged to the north by fragmentation caused by Canada Highway 3 and human settlement

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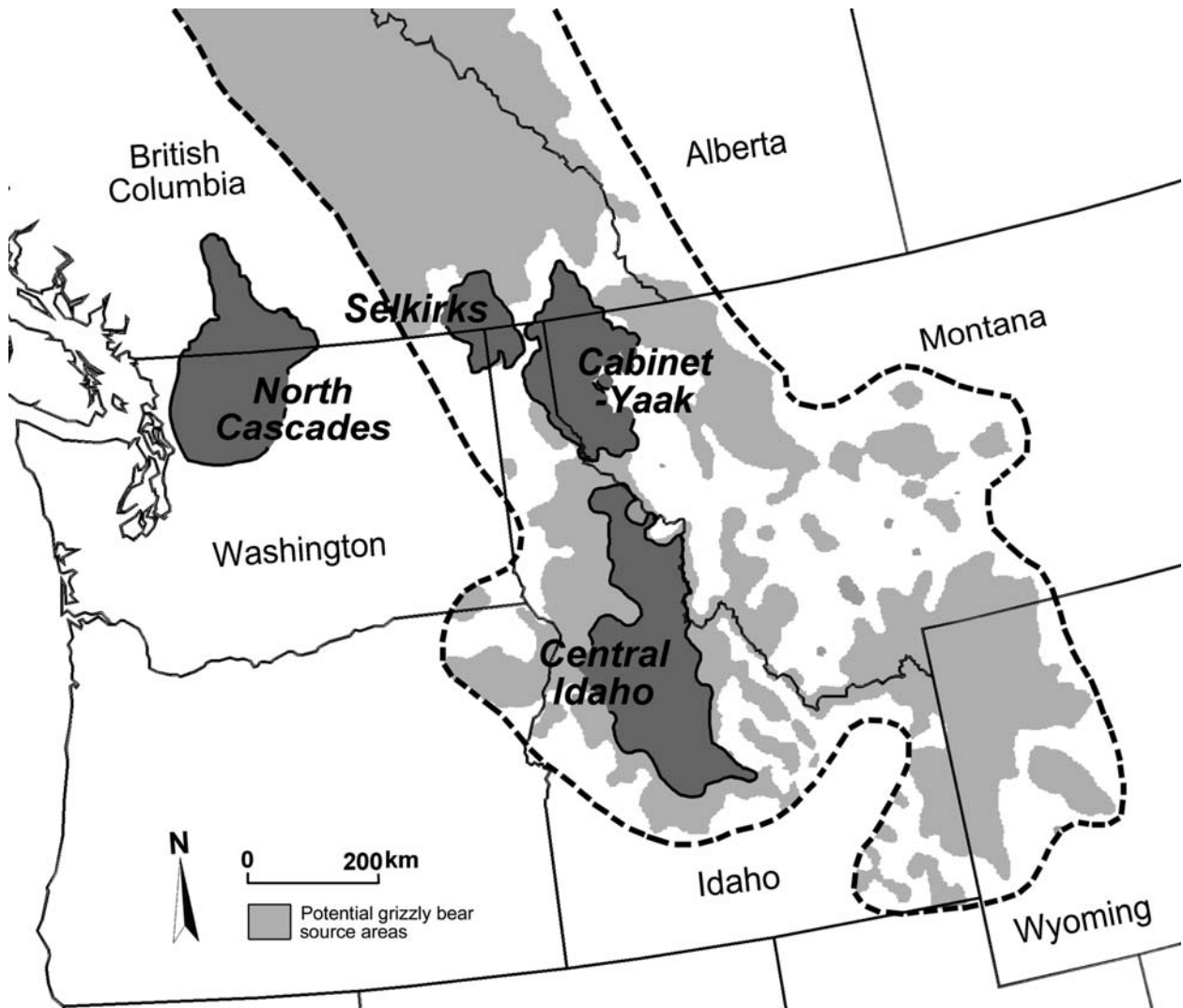[6]troy@ltb-ile.com

Fig. 1. Ranges of at-risk transboundary grizzly bear populations of western Canada and the USA and potential grizzly bear habitat in central Idaho (Merrill et al. 1999; dark gray), superimposed on modeled source areas for the Yellowstone-to-Yukon (Y2Y) region (in light gray, Y2Y region delineated by a dashed line; Merrill and Mattson 2003, Merrill 2004).

(Proctor et al. 2002). As in the North Cascades, grizzly bears in the Selkirk and Cabinet–Yaak regions exist at densities well below the potential for this region (<1 bear/100 km^2 compared to potentially 2–2.5 bears/100 km^2; Mattson and Merrill 2004). In the USA part of the Cabinet–Yaak, as many as 360 grizzly bears could be supported in an area currently occupied by <40 (Mattson and Merrill 2004). About 80 km south of the Cabinet–Yaak, in an area without known resident grizzly bears, central Idaho could support 300–600+ animals, depending on how available habitat is defined (Merrill et al. 1999, Boyce and Waller 2003, Merrill 2004).

The USA or BC governments consider these small or extirpated grizzly bear populations to be threatened (US Fish and Wildlife Service 1993, North Cascades Grizzly Bear Recovery Team 2001). Recovery plans for the North Cascade, Selkirk, and Cabinet–Yaak populations prescribe 3–10-fold increases in size (US Fish and Wildlife Service 1993, North Cascades Grizzly Bear Recovery Team 2001). Recent plans for the Bitterroot Mountains in central Idaho call for the restoration of about 300 bears (US Fish and Wildlife Service 2000).

Human-caused mortality during 1850–1950 was the primary cause of extirpations and severe reductions of

grizzly bear populations in central Idaho and transboundary regions of BC and the USA (North Cascades Grizzly Bear Recovery Team 2001, Mattson and Merrill 2002). Human-caused mortality continues to confound restoration efforts (Knick and Kasworm 1989, Wielgus et al. 1994, Wakkinen and Kasworm 2004). Restoration planning has naturally focused on limiting contact between humans and grizzly bears and reducing human lethality. However, restoration has had limited success. Despite efforts dating back 2–3 decades, including population augmentation, there has been little or no improvement in the status of transboundary grizzly bear populations (Kasworm et al. 1998, Wakkinen and Kasworm 2004). There are several possible explanations for this situation. In this paper we evaluate the hypothesis that American black bears (*Ursus americanus*) impede or otherwise complicate grizzly bear restoration, primarily through exploitation competition.

Management for restoration of at-risk grizzly bear populations has implicitly hypothesized that resident black bears do not affect grizzly bears (H_1). To our knowledge, there is no reference in recovery plans to potential negative effects of black bears on establishment, reproduction, or recruitment of grizzly bears. Here, we pose an alternate hypothesis (H_2): Where resident black bear populations are not heavily exploited and where diet overlap between black bears and grizzly bears is extensive, black bears reduce the odds of successful colonization by grizzly bears as well as the productivity of severely reduced grizzly bear populations, primarily through exploitation competition (Begon et al. 1990:198) and Allee effects (any positive relation between fitness and numbers of conspecifics [Stephens et al. 1999]).

We evaluate evidence relevant to whether H_2 or the hypothesis implicit in current management (H_1) is more defensible for restoration management of grizzly bear populations. We examine evidence related to (1) dietary overlap between North American grizzly and black bears, (2) life strategies, (3) direct or interference competition, (4) exploitation competition, and (5) distributions in North America. Our goal is not to reach definitive conclusions regarding the inter-specific ecology of black and grizzly bears, but to constructively broaden and refocus the discourse of grizzly bear restoration efforts.

Methods

We used weight of evidence (WOE) as our standard for reaching conclusions. Our use of WOE contrasts with traditional emphasis on minimizing type I errors in conventional scientific practice (erroneously concluding that an effect does exist). WOE also contrasts with minimizing type II errors (erroneously concluding that an effect doesn't exist) advocated in conservation applications (Shrader-Frechette and McCoy 1993). WOE is comparatively value neutral and, given the available evidence, roughly equates to determining which of several 'models' is the most defensible, or likely, representation of the world. In this regard, WOE has a conceptual tie to information theory and likelihood statistics (Smith et al. 2002). WOE is useful for judging alternate competing hypotheses when there is substantial uncertainty and yet a need to decide which version of competing realities to adopt as a basis for policy relevant decisions. WOE has been used for many purposes including assessments of sediment quality (Chapman et al. 2002) and ecological systems (Clark and Frid 2001, Springer et al. 2003).

We examined diet overlap between black and grizzly bears in western transboundary Canada and the USA, and between brown and black bears in Europe and eastern North America. In this paper we use brown bear to refer to *Ursus arctos* inhabiting Eurasia or coastal North America and grizzly bear to refer to *Ursus arctos* inhabiting interior North America. For the transboundary analysis we used results from 4 study areas where estimated fecal (scat) contents of both species were available (Tisch 1961, Shaffer 1971, Kendall 1986, Carriles 1990, Kasworm and Their 1991, McLellan and Hovey 1995). We used paired results from 3 additional study areas in drier regions north and south of the transboundary region (Hamer and Herrero 1983, Irwin and Hammond 1985, Raine and Kansas 1990, Mattson et al. 1991*a*, Aune 1994) as well as information on generalized rangewide diets (Mattson 1998) for contrast. As recommended by Abrams (1980), we used Schoener's index (Schoener 1968) to calculate diet overlap: $O_{jk} = 1 - \frac{1}{2}\Sigma| P_{ij} - P_{ik} |$, where P_{ij} is the proportion of species *j*'s feces comprised of item *i*, P_{ik} is the proportion of species *k*'s feces comprised of item *i*, and O_{jk} is total diet overlap (0 = none, 1 = complete). We used diet information for only hyperphagia (after mid-July; Mattson 1998) and classified fecal contents by 6 broad structural categories (foliage, roots, fleshy fruits, fat-rich fruits and seeds [e.g., acorns and pine seeds], invertebrates, and vertebrates; Mattson 1998).

We compared density and mean litter size, interbirth interval, age of primaparity, adult female body mass, and adult female range size of grizzly bear and black bear populations in interior North America to gain insight into differences in life strategies between the species. To do this, we compiled data from 29 grizzly bear and 30 black

bear populations, excluding areas with substantial runs of spawning coastal salmonids and black bear populations from west of the Cascade–Sierra Nevada crest in the co-terminous USA. We only considered black bear populations that were within current ($n = 15$) or former ($n = 15$) grizzly bear range in North America. The variation in methods among study areas, especially in estimating range size, limited the precision of our comparisons, so we based conclusions only on differences involving more standardized methods (such as measures of body mass) or order of magnitude.

Diet overlap

North American grizzly and black bears are large-bodied generalist omnivores with potentially substantial diet overlap (Herrero 1972, 1978; Mattson 1998). Ursid diets vary among regions depending on food availability and other ecosystem characteristics (Mattson 1998). Where starchy roots and tissue from vertebrates are abundant, grizzly bears tend to eat substantially more of both compared to sympatric black bears (Aune 1994, Jacoby et al. 1999, Hobson et al. 2000), and some grizzly bears obtain the majority of their energy from meat (Mattson 1997; Hilderbrand et al. 1999*a*, 1999*b*; Jacoby et al. 1999). Grizzly bears are physically adapted to excavating roots (Herrero 1978, Mattson 1998) and often dominate black bears at sites with concentrated energy-rich foods such as spawning salmonids or carrion from large-bodied carcasses (Barnes and Bray 1967, Craighead and Craighead 1971, Craighead et al. 1995).

In areas without abundant ungulates, spawning salmonids, or root foods, diets of grizzly and black bears converge. For example, in the western transboundary region of Canada and the USA, contents of black and grizzly bear scats were quite similar (Schoener's O, $\bar{x} = 0.86$, range = 0.84–0.89). This contrasts with typically lower similarity in drier study areas north and south of the boundary (Schoener's O, $\bar{x} = 0.69$, range = 0.54–0.86), and overlap of 0.77 and 0.65 between scat contents of American black bears, rangewide, and *Ursus arctos* in coniferous forest and arctic or alpine environments, respectively (Mattson 1998). Grizzly and black bears in the transboundary region depend almost wholly on fleshy fruits and succulent forbs for subsistence (Hilderbrand et al. 1999*b*, Jacoby et al. 1999)—primarily fruits of huckleberry (*Vaccinium membranaceum*), buffaloberry (*Shepherdia canadensis*), and juneberry (*Amelanchier alnifolia*), and foliage from grasses and sedges (*Carex* spp.), cow parsnip (*Heracleum lanatum*), scouring rush (*Equisetum arvense*), and other forbs (*Lathyrus ochro-*

leucus, *Angelica dawsonii*, *Ligusticum canbyi*, and *Osmorhiza* sp.). As a bottom line, the potential for competition between black and grizzly bears is especially high in regions, such as boreal forests and the trans-boundary of Canada and the USA, where vertebrates and root foods are relatively uncommon and fleshy fruits are abundant.

Life strategies

There were large differences between movements and individual and population-level demographic traits of American black and grizzly bears in current and former grizzly bear range (Tables 1–3). Compared to grizzly bears, black bears occurred at 8–11-fold higher densities (for populations in current and former grizzly bear range, respectively). On the other hand, adult female grizzly bears tended to have longer interbirth intervals (1.2–1.5 ×), were larger in size (1.6–2.3×) and used much larger ranges (4.7–5.1×) than adult female black bears. Cumulatively, these differences translated into higher annual *per capita* birth rates (1.3–1.4×) and much higher unit area population productivity (12–22×, in cubs/year/100 km^2) for black bears compared to grizzly bears. We found comparable differences in density (7.8×), body mass (1.9×), and range size (8.6×), even when considering only study areas ($n = 9$) with data for both species.

These results suggest that grizzly and black bears have intrinsically different demographic traits, evident even in shared ranges. Black bears can potentially fill a landscape with conspecifics rapidly because of orders-of-magnitude greater population productivity. Compared to grizzly bear populations, black bears populations can also respond more quickly to landscape-level changes in the location and quantity of resources. On the other hand, compared to individual grizzly bears, reproduction among individual black bears is predictably more sensitive to food availability, as a consequence of smaller body and range sizes (they have less somatic buffering; Lindstedt and Boyce 1985, Miller and Hickling 1990) and access to fewer potential resource patches. This prediction is consistent with numerous examples of food effects on annual reproduction of female black bears, primarily evident in reproductive failures following years of food scarcity (Jonkel and Cowan 1971, Rogers 1976, Eiler et al. 1989, Beck 1991, McLaughlin et al. 1994, McLean and Pelton 1994, Miller 1994, Costello et al. 2003). Of greatest relevance to this analysis, black bear populations have the capacity to use landscapes more intensively than sympatric grizzly bear populations. This potentiality is consistent with orders-of-magnitude higher rates of

Table 1. Demographic and movement parameters for North American grizzly bears in regions sympatric with black bears and without access to spawning salmonids.

Study area	Source	Demographic and movement parameters							
		Density (bears/ 100km^2)	Adult female mass (kg)	Adult female range (km^2)	Litter size	Litter interval (yrs)	Age of primaparity (yrs)	Reproductive rate[a] (n/yr)	Unit area reproductive rate[b] (n/yr/100 km^2)
Nelchina, Alaska	McLellan (1994)	1.0			2.1	3.8	5.6	0.55	0.14
Upper Susitna, Alaska	Miller et al. (1997) Miller (1984)	1.1		387					
Middle Susitna, Alaska	Miller et al. (1997)	2.7							
Prophet River, British Columbia	Poole et al. (2001)	1.6							
Parsnip Mountains, British Columbia	Hamilton and Austin (2002)	5.1							
Parsnip Mountains (plateau), British Columbia	Hamilton and Austin (2002)	1.2							
South Wapiti, Alberta	Alberta Forestry, Lands and Wildlife (1990)	0.7							
Berland, Alberta	Alberta Forestry, Lands and Wildlife (1990)	0.5							
Swan Hills, Alberta	Nagy and Russell (1978)	0.8	172	211					
Jasper National Park (NP), Alberta	Russell et al. (1979)	1.1							
Kananaskis, Alberta	Wielgus (1986)	1.4		248					
Southwest Alberta	Wielgus and Bunnell (1994)	1.6			1.4	3.0	5.5	0.47	0.19
Banff/Kananaskis, Alberta	Gibeau et al. (2001)			293					
Waterton NP, Alberta	Alberta Forestry, Lands and Wildlife (1990)	4.8							
Glacier NP, British Columbia	Hamilton and Austin (2002)	3.5							
Columbia Mountains	Hamilton and Austin (2002)	3.1							
Kootenay/Yoho NPs, British Columbia	Hamilton and Austin (2002)	0.9							
Central Selkirks, British Columbia	Mowat and Strobeck (2000)	2.7							
West Slopes, British Columbia	Hamilton and Austin (2002) Gibeau et al. (2001)	2.4		88					
Jumbo, British Columbia	Hamilton and Austin (2002)	2.5							
North Fork Flathead, British Columbia	McLellan (1994) Hamilton and Austin (2002) Hovey and McLellan (1996) McLoughlin et al. (1999)	4.8	114	200	2.2	2.8	6.4	0.79	0.94
North Fork Flathead, Montana	Jonkel (1978, 1980, 1982)			88					

Table 1. Continued.

Study area	Source	Demographic and movement parameters							
		Density (bears/ 100km^2)	Adult female mass (kg)	Adult female range (km^2)	Litter size	Litter interval (yrs)	Age of primaparity (yrs)	Reproductive rate[a] (n/yr)	Unit area reproductive rate[b] (n/yr/100 km^2)
South Selkirks, British Columbia, Idaho	Wielgus et al. (1994) Almack (1985)	2.3		325	2.2	3.0	7.3	0.73	0.42
South Fork Flathead, Montana	Jonkel (1978, 1980, 1982)	1.6	94		1.6	3.0	6.0	0.53	0.21
Glacier NP, Montana	Martinka (1974)	4.7			1.7				
Cabinet–Yaak, Montana	Kasworm et al. (2000, 2003)		129	574					
East Front, Montana	Aune and Kasworm (1989) Aune (1994)	0.7	135	642	2.2	2.6	6.0	0.85	0.15
Mission Mountains, Montana	Servheen (1983)	2.0		285					
Yellowstone, Montana, Wyoming	Blanchard (1987) Blanchard and Knight (1991) Pease and Mattson (1999)	1.6	135	281	2.4	2.6	5.6	0.92	0.37
N		26	7	11	8	7	7	7	7
Mean		2.2	124	321	2.0	3.0	6.1	0.69	0.34
SD		1.4	28	154	0.3	0.4	0.6	0.16	0.26

[a]Litter size/litter interval.
[b]Reproductive rate × density.

capture or detection for black compared to grizzly bears in several study areas (e.g., Aune and Kasworm 1989, Kasworm et al. 2000, Romain-Bondi et al. 2004).

Higher densities, smaller ranges, and higher population-level productivity also mean that black bear populations have an intrinsic advantage over grizzly bear populations when subject to exploitation by humans. Black bear populations are better able to absorb periods of heavy exploitation and can more rapidly recover. Perhaps most important, if there is spatial structure to exploitation, including the existence of areas where death rates are low (refuges), black bear populations will more likely exhibit a sustainable source–sink structure compared to sympatric grizzly bear populations (Doak 1995, Woodroffe and Ginsberg 1998). The comparative vulnerability of grizzly bear populations to human exploitation, rooted in general demographic traits alone, is consistent with the widespread persistence of black bears in areas where grizzly bears were extirpated (Pelton et al. 1998, Woodroffe and Ginsberg 1998, Mattson and Merrill 2002). Human-caused deaths and exploitation competition with black bears potentially interact synergistically to the detriment of grizzly bears.

Interference competition

Grizzly bears typically have the advantage over black bears in interference or resource defense (Begon et al. 1990) competition for food. Where bears concentrate at predictable energy-rich food sources such as salmonid spawning streams, large-bodied ungulate carcasses, or garbage disposal areas, grizzly and brown bears dominate feeding opportunities, excluding most black bears (Barnes and Bray 1967, Craighead and Craighead 1971, Craighead et al. 1995). Grizzly bears can also exclude black bears from lower quality food patches (Russell et al. 1979, Hamer and Herrero 1983). Access is determined largely by factors such as body size and level of aggression (Stonorov and Stokes 1972, Egbert and Stokes 1976, Herrero 1983, Craighead et al. 1995), both of which favor adult grizzly bears (Herrero 1972, 1978). If a black bear ventures among concentrated grizzly bears, usually it is a large adult male (Barnes and Bray 1967, Craighead and Craighead 1971). Grizzly bear predations on black bears have been recorded, highlighting the risk run by sympatric black bears (Ross et al. 1988, Mattson et al. 1992, Smith and Follmann 1993, Boyd and Heger 2000, Bertram and Vivion 2002, Gunther et al.

Table 2. Demographic and movement parameters for American black bears in regions currently occupied by grizzly bears and with little access to spawning salmonids.

Study area	Source	Density (bears/100km²)	Adult female mass (kg)	Adult female range (km²)	Litter size	Litter interval (yrs)	Age of primaparity (yrs)	Reproductive rate[a] (n/yr)	Unit area reproductive rate (n/yr/100 km²)
Kenai 1947, Alaska	Schwartz and Franzmann (1991) Miller et al. (1997)	19.9			2.2	2.2	5.8	1.00	4.98
Kenai 1969, Alaska	Schwartz and Franzmann (1991) Miller et al. (1997)	28.9			2.3	2.1	4.6	1.10	7.91
Susitna, Alaska	Miller et al. (1997) Garshelis (1994)	8.9		87	2.1	2.7	5.9	0.78	1.73
Eastern interior, Alaska	Bertram and Vivion (2002)		63	16	2.1	1.6	9.0	1.31	
Berland, Alberta	Alberta Forestry, Lands and Wildlife (1993)	0.9							
Swan Hills, Alberta	Nagy and Russell (1978)	1.8	80	122					
Banff NP, Alberta	Alberta Forestry, Lands and Wildlife (1993) Hebblewhite et al. (2003)	0.8			1.9	2.0	5.0	0.95	0.19
Sheep River, Alberta	Alberta Forestry, Lands and Wildlife (1993)	23.3							
North Fork Flathead, Montana	Jonkel and Cowan (1971) Jonkel (1978, 1980, 1982)	45.0	54		1.7	3.0	7.0	0.57	6.38
Priest Lake, Idaho	Rohlman (1989)	34.4			1.5				
Northwest Montana	Kasworm and Manley (1988) Kasworm and Thier (1994)		69	24	1.8	3.2	6.0	0.56	
Okanogan, Washington	Koehler and Pierce (2003)			26					
South Fork Flathead, Montana	Jonkel (1978, 1980, 1982)		53						
East Front, Montana	Aune (1994)		58	137					
South-central Montana	Mack (1988)		54	33					
N		9	7	7	8	7	7	7	5
Mean		16.4	55	63	2.0	2.4	6.2	0.89	4.24
SD		15.2	9	47	0.3	0.5	1.4	0.26	2.87

[a]Litter size/litter interval.
[b]Reproductive rate × density.

2002). By contrast, there are no published records of a black bear killing a grizzly bear.

Black bears apparently avoid risk of physical injury from grizzly bears by avoiding grizzly bears concentrated at feeding sites. This type of avoidance has been documented in the Yellowstone ecosystem around cutthroat trout (*Oncorhynchus clarki*) spawning streams and ungulate winter ranges in Yellowstone National Park (Reinhart and Mattson 1990, Green et al. 1997), on cattle grazing allotments (Holm et al. 1999), at cutworm moth (*Euxoa auxiliaris*) aggregation sites (Mattson et al. 1991b, French et al. 1994) and, in decades past, around dumps (Barnes and Bray 1967). Black bears are probably not very competitive where high-quality foods are

Table 3. Demographic and movement parameters for western American black bears in regions formerly occupied by grizzly bears and east of the Cascade–Sierra Nevada crest.

Study area	Source	Density (bears/ 100km²)	Adult female mass (kg)	Adult female range (km²)	Litter size	Litter interval (yrs)	Age of primaparity (yrs)	Reproductive rate[a] (n/yr)	Unit area reproductive rate[b] (n/yr/100 km²)
Idaho	Amstrup and Beecham (1976) Garshelis (1994)	43.0		34	1.7		5.0		
West-central Idaho	Beecham (1980) Reynolds and Beecham (1980)	77.0		18	1.9	2.4	4.8	0.79	15.24
Snowy Range, Wyoming	Grogan and Lindzey (1999)	2.5							
Northwest Colorado	Grogan and Lindzey (1999)	36.0							
North-central Colorado	Grogan and Lindzey (1999)	8.0							
Black Mesa, Colorado	Beck (1991)	15.4	80		1.6	2.0	4.7	0.80	3.08
East Tavaputs, Utah	Tolman (1998)				2.0	2.0	5.5	1.00	
La Sal Mountains, Utah	Tolman (1998)		74		2.0	1.8		1.11	
Central Utah	Bates (1991)		104	41					
Northern New Mexico	Costello et al. (2001)	17.0	69	123	1.8	1.8	5.7	1.00	4.25
Southern New Mexico	Costello et al. (2001)	9.4		172					
North of Mogollon Rim, Arizona	LeCount (1987)	6.0							
East-central Arizona	LeCount (1990)	14.3			2.0		5.0		
Four Peaks, Arizona	LeCount (1990) LeCount (1982, 1990)	33.0		18	1.9		5.0		
Southeast Arizona	Waddell and Brown (1984a,b)	28.2	56						
n		12	5	6	8	5	7	5	3
Mean		24.2	76	68	1.9	2.0	5.1	0.94	7.52
SD		20.2	16	59	0.1	0.2	0.3	0.12	5.48

[a]Litter size/litter interval.
[b]Reproductive rate × density.

concentrated at predictable times and places, and thus can be dominated by resident grizzly bears.

Exploitation competition

Scramble or exploitation competition (Begon et al. 1990) from black bears could adversely affect grizzly bears where there is substantial diet overlap, moderately dispersed food resources (at the scale of black bear annual ranges), and high black bear densities. These conditions are potentially commonplace, especially in parts of interior North America where ungulates and salmonids are absent or comparatively rare, typically at mid-latitudes in areas with wet maritime climates. Given this potential, there are additional factors that can increase the competitive advantage of black bears over

grizzly bears. Foraging trials with captive black and grizzly bears have shown that bears >100–120 kg in size gain less absolute weight than smaller bears fed berries or herbaceous vegetation (Welch et al. 1997, Rode et al. 2001). Weight gain by large bears was constrained more by reduced foraging efficiency than by energy or nutrient concentrations. In contrast to small bears, large bears depend more on food plants that allow for large bite sizes and high bite rates. Of relevance to size-dependent foraging efficiency, adult female grizzly bears average 125 kg whereas adult female black bears average 55 and 76 kg in interior regions where these 2 species are or were sympatric, respectively (Tables 1–3).

Size-dependent foraging efficiencies potentially interact synergistically with differences in range sizes and

population densities of black and grizzly bears. The foraging trials cited above suggest that black bears, in contrast to grizzlies, can subsist on poorer-quality patches of berries and herbaceous vegetation. This presumably facilitates the survival of black bears in smaller ranges with fewer rich food patches. On the other hand, high densities of black bears in which each intensively uses a small range increase the odds that a black bear, rather than a grizzly, will find and exploit the rich patches that do exist. A grizzly bear that encounters a rich patch will likely dominate it, but any time spent feeding after foraging efficiencies have peaked could mean that other potentially profitable patches will be made less profitable by black bears. This scenario would be especially relevant to grizzly bears if rich foods, like huckleberries, are abundant and at peak quality for only a short time. Heavy consumption of both forbs and fleshy fruits by bears in transboundary Canada and the USA is typically restricted to 2-month periods each; June–July for forbs and August–September for fleshy fruits (McLellan and Hovey 1995).

Logically, exploitation competition with black bears would potentially limit reproduction of grizzly bears only if food eaten by black bears would otherwise be eaten by grizzly bears. This raises the question of whether competition with black bears is trivial relative to competition with other smaller and potentially much more numerous herbivores (such as deer) and frugivores (such as birds). Consumption of bear foods by non-ursid species matters in this analysis to the extent that this type of consumption is positively correlated with patch quality reckoned in terms meaningful to a bear, and this consumption systematically varies at a scale broad enough to explain historic grizzly bear distributions (see below). If these 2 conditions do not hold, then consumption of bear foods by non-ursid species would be a random, or non-explanatory, effect. Put another way, it is patch quality rather than food abundance *per se* that matters most in assessing the effects of competitors. Grizzly bears require extremely high quality patches of berries and forbs to make energetic gains (Welch et al. 1997, Rode et al. 2001). Regardless of consumption by other species, if black bears select for the same kinds of high quality patches as grizzlies, then black bears will have a disproportional effect compared to other species with different selection profiles. As a bottom line, simply measuring who's consuming how much of what, without differentiating species-relevant definitions of patch quality, is not an adequate basis for concluding who is likely affecting whom through exploitation competition.

For purposes of this appraisal, exploitation competition with black bears also matters to the extent that food availability affects reproductive rates of female grizzly bears. Because of large range and body sizes, grizzly bears are likely better able than black bears to average-out annual variability in food supplies. If so, interannual variability of reproduction would be less for female grizzly bears compared to female black bears in the same environment. However, a lack of interannual variability does not equate to lack of lifetime or population-level effects of food on grizzly bear demography. Detection of food effects depends on comparative analyses of population-level phenomena such as density, or, in the case of individual-level effects, long-duration studies involving large numbers of marked animals. The few published studies of this nature have shown a substantial effect of food on grizzly bear demography. Grizzly bear population densities in Alaska vary by an order of magnitude, primarily as a function of access to anadromous salmon (Salmonidae; Miller et al. 1997). Relatedly, female grizzly bears with access to ungulate tissue or salmon in Alaska tend to be more productive than females without (Reynolds and Garner 1987, Hildebrand et al. 1999*b*). In the contiguous USA, there are strong positive relations between consumption of whitebark pine (*Pinus albicaulis*) seeds and age of first reproduction, reproductive interval, and litter size (Mattson 2000, Schwartz et al. 2005). These results are consistent with positive relations between growth and diet quality (Welch et al. 1997, Rode et al. 2001) and positive relations between population-averaged female body mass and reproduction (Stringham 1990, Hilderbrand et al. 1999*b*). Reckoned in terms of lifetime reproductive success and population density, it is more defensible to conclude that food availability affects grizzly bear demography than to conclude otherwise, in which case, exploitation competition with black bears matters.

Dispersal and Allee effects

Numerous theoretical studies have suggested that Allee effects, in combination with factors such as dispersal potential and exploitation competition, can determine whether populations establish and persist (Keitt et al. 2001, South and Kenward 2001, Etienne et al. 2002). An extreme Allee effect is colonization by males alone, in which case fitness is zero. Successful colonization obviously depends on the ability of females to arrive, survive, and reproduce. Similarly, recovery of depressed populations requires both adequate survival and reproduction. Genetic evidence suggests that male brown bears readily cross water barriers roughly 7 km wide and maintain broad scale genetic mixing on the

mainland (Paetkau et al. 1998). However, female grizzly and brown bears appear to be confined by water barriers as narrow as 2–4 km and contribute so little to gene flow that matrilineal clades have maintained relatively well defined geographic boundaries for thousands of years, even on the mainland (Paetkau et al. 1998, Waits et al. 1998, Shields et al. 2000). This genetic evidence is consistent with observations of grizzly bear dispersal that reported gender-bias. Young males dispersed an average 30–70 km (Blanchard and Knight 1991, McLellan and Hovey 2001), whereas young females tended to be highly philopatric (Mace and Waller 1998, McLellan and Hovey 2001). Philopatry apparently limits female grizzly bear dispersal, which together with human-caused mortality and competition from black bears could substantially limit the ability of grizzly bears to colonize new range. Extreme low densities of conspecifics (<0.5–1 bear/100 km^2, as in the North Cascade and Cabinet–Yaak regions [Mattson and Merrill 2004]) could also reduce the odds of a female finding a mate (an Allee effect), in turn reducing population productivity.

Distributions in North America

The material reviewed so far provides a basis for evaluating, in theory, whether black bears could adversely affect grizzlies. This begs the question: is there direct evidence for an effect of black bears on either the distribution or abundance of grizzly bears? We are aware of 2 distributional anomalies that have bearing on this issue.

Eastern deciduous forests

With the exception of a limited zone of contact in Pacific coastal Pleistocene refugia (Heaton et al. 1996, Stone and Cook 2000), grizzly bears and American black bears were isolated from each other until about 12–13,000 years before present (bp; Kurtén and Anderson 1980). Grizzly bears were restricted to Eurasia and Beringia, north and west of North America's Pleistocene continental ice sheets, whereas American black bears were restricted to areas to the south. With melt of the ice sheets around 13,000 years bp, grizzly bears invaded from the north, out of Beringia (Kurtén and Anderson 1980), and possibly from the west, out of coastal refugia (Mustoe and Carlstad 1995). At the same time, American black bears spread north. During these invasions, vegetation changed from what had been largely continuous coniferous forests and woodlands south of the Pleistocene ice sheets (Wright 1981, Thompson and Mead 1982, Webb 1988) to modern east–west trending boreal forests of Alaska and Canada, north–south trending deciduous forests of eastern North America and mid-continent grasslands (Barbour and Billings 1988; Fig. 2a).

Despite the passage of 12–13,000 years, grizzly bears never established themselves in eastern deciduous or boreal forests of North America, or if they did, they were extirpated prior to the arrival of Europeans (Fig. 2b). There are disputed claims of grizzly bear fossils from eastern North America, some of which have been attributed to mistaken identification of large-bodied black bears from the late Pleistocene and early Holocene (Kurtén and Anderson 1980). Regardless, the implications are the same for potential adverse effects of American black bears on grizzly bears. Absence of grizzly bears from eastern North America is anomalous for several reasons. First, the grizzly bear invasion was asymmetrical, reaching as far south as northern Mexico, but only as far east as the Great Plains. Second, other post-Pleistocene Beringian invaders, such as moose (*Alces alces*) and technologically advanced humans (Kurtén and Anderson 1980), spread across the boreal forest and, in the case of humans, to the southern tip of South America. Third, *Ursus arctos* can exist at high densities in deciduous forests like those of eastern North America. This is clearly demonstrated by brown bears in temperate Europe (Zedrosser et al. 2001), which subsist on diets not much different from the diets of American black bears in temperate North America. Considering pairwise overlap of fecal contents from 11 European brown bear and 11 eastern American black bear populations, 18% were >80% similar and 46% were >70% similar (Table 4). Inferred diets were most alike between black bears in Vermont, Michigan, Wisconsin, and the Smoky Mountains, and European brown bears in Greece, Yugoslavia, the Carpathian Mountains, and the southern Urals. The boreal and deciduous forests of eastern North America are not intrinsically inhospitable to grizzly bears, nor would it have been impossible, on the basis of mobility, for potentially large numbers of grizzly bears to reach eastern North America prior to the arrival of Europeans.

Competition from resident American black bears, together with mortality caused by newly arrived humans, is the most plausible explanation for an absence or near absence of grizzly bears in eastern North America. The nature of North America's boreal forests and the orientation and nature of central North America's grasslands would have exacerbated the effects of competition with black bears. North American boreal forests support some of the lowest documented grizzly bear densities (<1 bear/100 km^2; see Table 1) while, in places, supporting 30–40 black bears/100 km^2 (Fuller and Keith
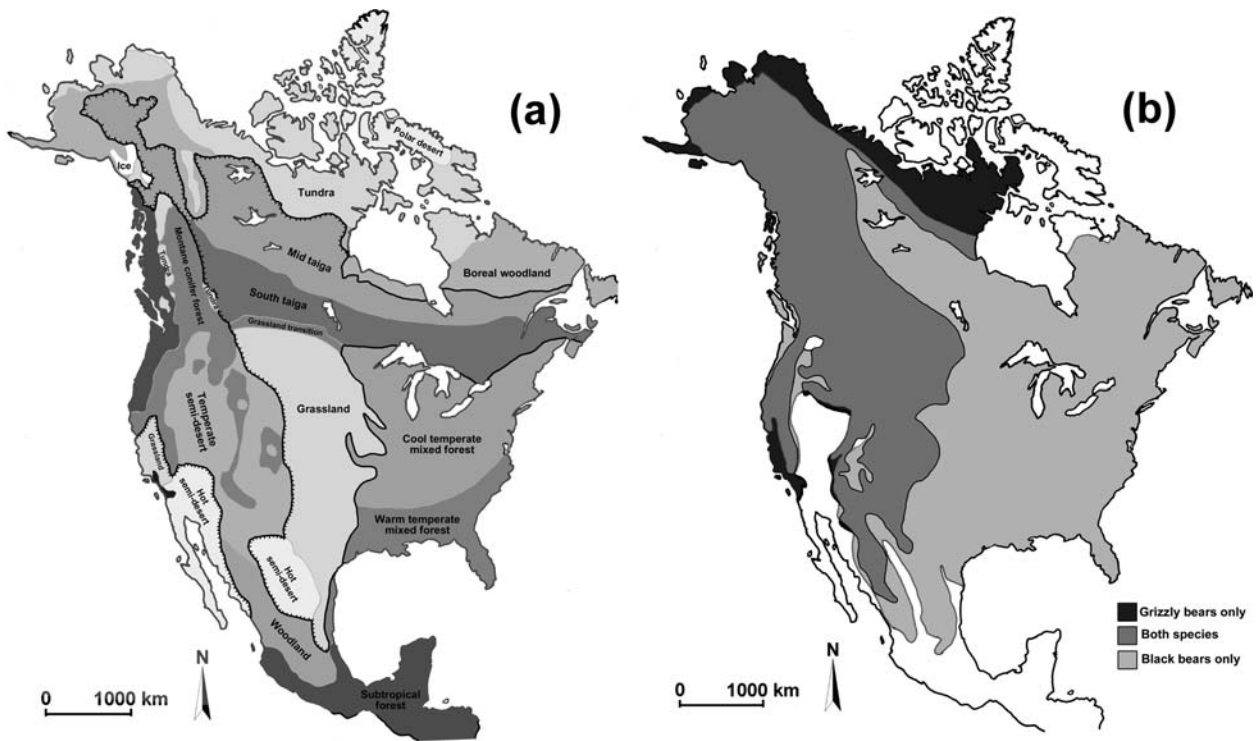
Fig. 2. (a) Modern vegetation zonation in North America (Adams and Faure 1997), and (b) approximate ranges of grizzly bears and American black bears in North America during the early 1800s (Pelton et al. 1998, Mattson and Merrill 2002). In (a), vegetation formations hypothesized to pose a barrier to grizzly bear invasion (i.e., taiga, grassland, and hot semi-desert [Mattson and Merrill 2002]) are delineated by a solid black line that is crenellated in directions facing grizzly bears invading from the north or west.

1980, Pelchat and Ruff 1986). North American boreal forests are also less productive than Siberian boreal forests, primarily because they lack stone pine (*Pinus sibirica* and *P. pumila*) seeds, the defining food of Siberian brown bears (Mattson and Jonkel 1990). In the North American Great Plains, productive bear habitats, including historical concentrations of bison (*Bison bison*) carrion, were localized along serpentine east–west trending riverine habitats (Cutright 1969, Mattson and Merrill 2002, Laliberte and Ripple 2003). This configuration would have funneled grizzly bears into restricted habitats already occupied by black bears and already or soon to be occupied by village-dwelling Native Americans (Driver 1969). Native Americans periodically killed grizzly bears (Hallowell 1926, Ewers 1958, Mathews 1961), black bears potentially compete with grizzlies, and black bear populations can better sustain human-caused mortality. These factors likely gave black bears a competitive advantage in the boreal forests and along the rivers of the Great Plains, perhaps sufficient to have slowed or curbed the eastward expansion of grizzly bears.

Pacific coastal islands

The distribution of ursids on Pacific coastal islands of Alaska and BC, Admiralty south to Vancouver, provides additional evidence for potential competitive exclusion of grizzly and brown bears by black bears. Most islands support only one species, with brown bears alone on Admiralty, Baranof, and Chichagof (ABC) Islands to the north, and black bears alone on most islands from Prince of Wales south (Fig. 3). This pattern exists despite (1) during the Pleistocene, *Ursus arctos* and American black bears coexisted on Prince of Wales Island and other potential coastal refugia (Heaton et al. 1996, Byun et al. 1997), (2) many islands exclusively inhabited by black bears are within a few km of mainland areas occupied by brown bears, and (3) brown bears have been known to swim up to 34 km to forage on remote islands (Bailey and Faust 1984; T. Smith, US Geology Survey Alaska Science Center, Anchorage, Alaska, USA, personal communication, 2003). During 2003, a male brown bear was observed on northern Vancouver Island, presumably after swimming from the mainland (Fong 2003).

Table 4. Pairwise similarity of bear fecal contents (Schoener's *O*) from American black bear study areas in eastern temperate North America and brown bear study areas in temperate Europe. Sources are given in Mattson (1998) except for citations added to the Mattson (1998) database for this analysis, which are identified by superscripts. Cells in bold face identify similarities ≥0.8 and cells in italics similarities ≥0.7.

European brown bear study areas	Eastern North American black bear study areas										
	Arkansas[a]	Great Smokies 1	Great Smokies 2	Maine	Vermont	Wisconsin 1[b]	Michigan[c]	Wisconsin 2	Pennsylvania	Shenandoah, VA	Western VA
Abruzzo, Italy	0.47	0.66	0.67	0.64	0.69	*0.73*	*0.79*	*0.76*	0.47	0.48	0.44
Pyrennes, Spain	**0.83**	*0.71*	0.58	0.63	0.65	*0.73*	*0.74*	*0.74*	0.57	0.50	0.46
Western Greece[d]	**0.88**	**0.81**	*0.70*	*0.77*	*0.79*	*0.77*	*0.75*	*0.76*	0.66	0.61	0.57
Yugloslavia	*0.70*	*0.78*	**0.82**	**0.82**	**0.85**	*0.78*	*0.77*	0.66	*0.79*	*0.77*	*0.71*
Polish Carpathians[e]	*0.73*	**0.83**	*0.73*	**0.80**	**0.92**	**0.82**	**0.82**	*0.71*	0.69	0.63	0.59
Southern Urals, Russia	0.62	*0.79*	0.69	0.69	**0.83**	**0.84**	**0.85**	**0.81**	0.59	0.52	0.47
Carpathians	0.59	*0.77*	0.68	0.67	*0.79*	**0.82**	**0.85**	*0.76*	0.57	0.51	0.46
Northern Norway[f]	*0.74*	0.69	0.59	0.65	**0.81**	*0.79*	**0.85**	**0.85**	0.54	0.50	0.46
Scandinavia (no sheep)[g]	0.57	0.69	0.65	0.68	0.69	**0.83**	**0.84**	0.76	0.56	0.53	0.47
Norway	0.58	*0.70*	*0.70*	*0.75*	*0.76*	**0.84**	*0.78*	0.67	0.57	0.59	0.54
Scandinavia (sheep)[g]	0.32	0.45	0.46	0.49	0.54	0.58	0.61	0.53	0.31	0.33	0.29

[a]Clapp (1986).
[b]Norton (1981).
[c]DeBruyn (1992).
[d]Vlachos et al. (2000).
[e]Frąckowiak (1997).
[f]Persson et al. (2001).
[g]Dahle et al. (1998).

The mutually exclusive distribution of black and brown bears on coastal islands has a likely mechanistic explanation. Gender-biased dispersal creates the potential for synergistic interaction between Allee effects and competition from black bears to the detriment of colonizing brown bears, especially in situations where humans kill any number of brown bears. To the extent that body size is a factor in interference competition, the comparatively large size of ancestral and contemporary coastal black bears (Nagorsen et al. 1995) probably gives them an additional edge, especially in confronting smaller brown bears such as dispersing subadult males. Whatever the initial historical reasons, once established, the pattern of Pacific coastal island occupancy by black and brown bears probably has been perpetuated by Allee effects and competition.
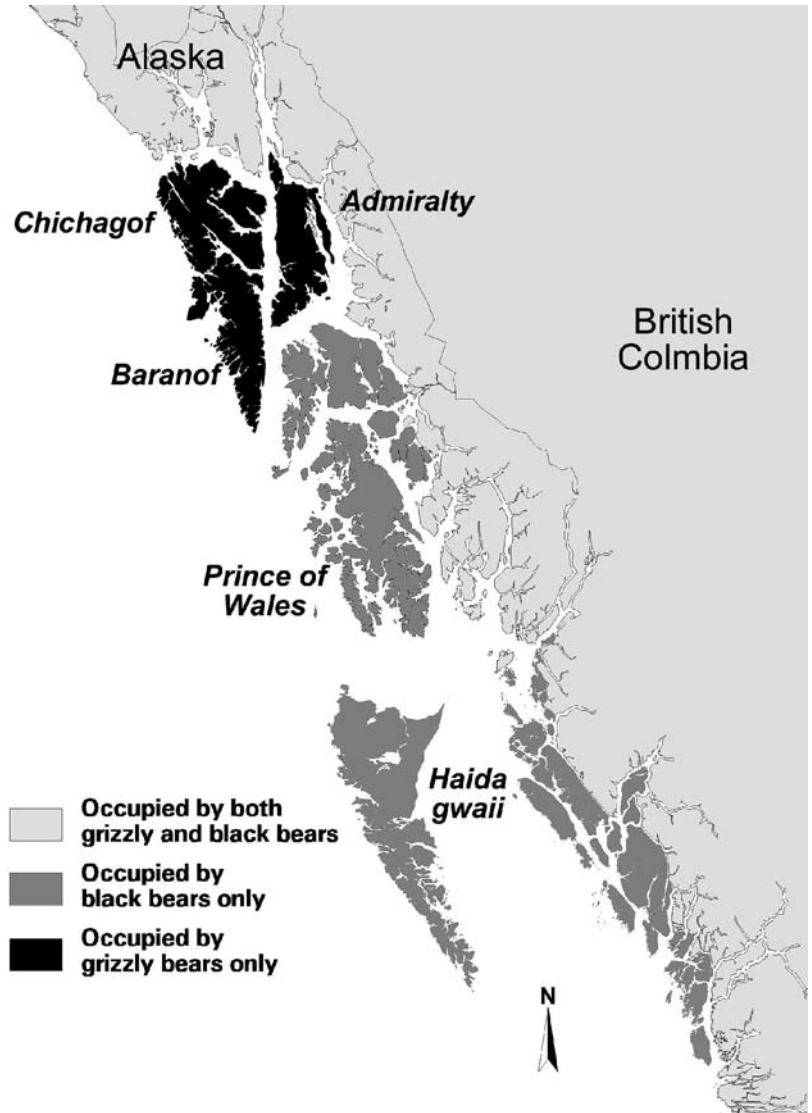
Synthesis

In a broad sense, grizzly bears and American black bears are each better adapted to different environments. The large ranges and body sizes of grizzly bears allow them to survive in environments with widely dispersed and annually variable foraging opportunities (Herrero 1978). Long front claws and well-developed supra-scapular muscles also allow grizzly bears to effectively exploit excavated foods such as roots and ground squirrels (*Spermophilus* sp.; Herrero 1978, Mattson 1998). These adaptations match the exigencies of steppe tundra environments in Pleistocene Eurasia and Beringia (Herrero 1972, 1978; Kurtén and Anderson 1980; Grichuk 1984; Markova 1984; Vereshchagin and Kuz'mina 1984). The smaller individual ranges and higher densities and population productivities of American black bears allow them to better exploit population-level, decadinal variation in habitat productivity attributable to phenomena such as stand replacement forest fires and forest succession. Smaller body size and shorter, more curved claws also allow black bears access to tree canopies for security and food (Herrero 1972, 1978). These adaptations match the opportunities of

formative forested environments as well as Pleistocene threats attributable to large-bodied carnivores such as American lions (*Panthera leo atrox*) and Tremarctine bears (*Arctodus simus* and *A. floridanus*; Herrero 1972, 1978; Kurtén and Anderson 1980).

The weight of evidence presented here supports some tentative conclusions regarding interactions of sympatric black and grizzly bears. Grizzly bears very likely have an advantage over black bears, as individuals and populations, where high quality foods are concentrated at predictable times and places. This would allow grizzly bears to dominate high quality foraging opportunities through interference or resource defense competition, especially meat resources such as spawning salmonids, bison carrion, and moose and elk (*Cervus elaphus*) killed outright. In contrast, black bear populations would have an advantage over grizzly bears where high quality foods are more dispersed and less predictable (within years and at the scale of black bear annual ranges), typically where fleshy fruits and succulent forbs form the bulk of both species' diets. They would also have an advantage where food (hard and soft mast) was concentrated in tree canopies. Under these circumstances, black bears would be in a better position to exploit high quality foraging opportunities because of their much higher population densities, more intensive use of smaller ranges, and ability to climb trees. Black bears would also be able to subsist on lower quality patches of fleshy fruits

Fig. 3. Distributions of grizzly bears and American black bears on islands and the mainland of Pacific coastal Alaska, USA, and British Columbia, Canada (data from Tom Smith, US Geological Survey Alaska Science Center, Anchorage, Alaska, USA, and Matt Austin, Ministry of Water, Land and Air Protection, Biodiversity Branch, Victoria, British Columbia, Canada).

and foliage because of greater foraging efficiencies associated with their smaller size. Where shared vegetal foods are moderately dispersed and moderately unpredictable, a black bear would likely find and exploit a food patch before a grizzly bear, to the point where it was unprofitable to grizzly bears that follow. By contrast, a high quality patch exploited and vacated by a grizzly bear would likely still be profitable to a black bear.

If present, demographic effects of exploitation competition with black bears would manifest in reduced grizzly bear reproduction. If biologically significant, exploitation competition could forestall compensatory increases in productivity of declining grizzly bear populations or high levels of reproduction among low-density colonizers. Because of low resilience (Weaver et al. 1996), even small effects on productivity could be important if humans killed any number of adult grizzly

bears. With people present and killing bears, grizzlies would be more vulnerable than black bears to any increase in death rate, and the competitive advantage of black bears would be enhanced. With black bears present, the effects of human-caused mortality would be exacerbated. This synergism may explain the absence or near absence of grizzly bears in eastern North America and the absence of brown bears on a number of large Pacific coastal islands occupied by both humans and black bears since the early Holocene.

If our appraisal is correct, there are implications for colonizing or severely reduced grizzly bear populations. If resident black bear populations are near carrying capacity and the ursid diet is primarily forbs and fruits, grizzly bears will probably have a difficult time invading new areas because of gender-biased dispersal and exploitation competition from resident black bears. If humans kill colonizing grizzly bears, the difficulties will be compounded. For resident low-density grizzly bear populations, exploitation competition with black bears could depress reproductive rates and forestall compensatory increases that might otherwise allow escape from an extinction vortex. Our appraisal suggests that transboundary populations of BC and the USA might not respond well to even substantial reductions in human-caused mortality, and that natural invasion of central Idaho from the north might never occur, even with remediation of sub par habitat conditions between central Idaho and the Cabinet Mountains. With respect to the hypotheses we posed in this paper, the weight of evidence presented here does not support H_1, the hypothesis implicit to current management. Rather, the evidence supports H_2: Where resident black bear populations are not heavily exploited and where diet overlap between black bears and grizzly bears is extensive, black bears reduce the odds of successful colonization by grizzly bears as well as the productivity of severely reduced grizzly bear populations, primarily through the interaction of exploitation competition and Allee effects.

Research implications

There is only circumstantial evidence for black bears affecting grizzly bear population recovery in transboundary regions of western Canada and the USA. Adopting the perhaps dubious traditional scientific emphasis on avoiding type I rather than type II errors (Shrader-Frechette and McCoy 1993), there are several research designs that could test the existence, nature, and magnitude of a black bear effect. One approach would employ monitoring movements and demography of

grizzly bears in a minimum of 2 study areas with comparable environments, one treated by the near complete removal of black bears, and the other providing control by leaving black bears intact. Such a study could be latitudinal as well, by monitoring grizzly bears pre- and post-black bear removal in the treatment area. However, there are ethical and logistical problems with such a design. Certain interest groups could legitimately argue that it is unethical to temporarily extirpate a wildlife population for research purposes. Logistically, it would be difficult to control factors such as natural variation in foods and variation in human-caused mortality. Because our hypothesis is specific to colonizing or severely reduced grizzly bear populations, small sample sizes would also provide only limited power to detect effects.

Another research design would entail detailed study of food availability and individual bear movements. Food abundance would be monitored inside paired exclosures (treatments) and freely accessible areas (controls), over a range of patch conditions, to determine whether food was limiting and, if so, under what circumstances. Close monitoring of black and grizzly bears with GPS (global positioning system) technology, real-time data delivery, and timely follow-up site investigations could reveal which species and which individuals were accessing what kinds of patches. Both designs described here would be expensive and difficult to implement, especially if emphasis was placed on accumulating sufficient sample sizes. However, hard to measure is not the same as unimportant.

Management implications

According to one ideal of governance, government agents should adopt the most defensible representation of managed systems to make decisions in service of the common good that account for prescribed policy and different human interests (Clark 2002). If H_2 is a more defensible representation than H_1 of the natural system affecting restoration of at-risk or extirpated grizzly bear populations in west central North America, then there are implications for management. On a per bear basis, the job of restoration is predictably more difficult than that of conserving grizzly bear populations in places such as the Yellowstone region of Wyoming, Montana, and Idaho, or the East Front of the Alberta Rocky Mountains. Measures taken in the transboundary region would have less *per capita* efficacy. Put in concrete terms, if H_2 is "true," managers of transboundary populations would need to consider extreme measures such as: (1) setting prescribed limits for human-caused mortality much lower than in

other regions, perhaps at or near zero; (2) major, rather than experimental, augmentations of resident grizzly bear populations; (3) major reductions of resident black bear populations; and (4) enhancement of habitat components (ungulates and roots and berries in certain subalpine habitats) known to be important and primarily exploited by grizzly bears. Each option would pose a major challenge and its own set of complications. Major reductions of black bear populations would perhaps be the least desirable measure, primarily because of costs to human interests that value the existence of black bears or black bear sport hunting. A major kill of black bears would also pose the challenge of insuring that grizzly bears were also not killed by accident—already a significant issue in transboundary regions (Knick and Kasworm 1989, Wielgus et al. 1994, Mace and Waller 1998, McLellan et al. 1999). In any case, managers and agency biologists will judge the merits of our analysis for themselves, and any adopted measures will hopefully be the outcome of a process that adequately judges policy fulfillment and costs and benefits to various human interest groups.

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