How vulnerable are denning bears to disturbance?

John D. C. Linnell, Jon E. Swenson, Reidar Andersen, and Brian Barnes

Abstract When exposed to human disturbance, most large carnivores are able to move away from the source with little energetic cost. Bears represent an exception in that during winter, most individuals spend several months in an energy-saving state of hibernation in a den. This implies that disturbance of denning bears has the potential to have a large energetic cost, although data on the subject are rather diffuse. We reviewed the literature on den-site selection, denning physiology, and responses to disturbance for the brown bear (*Ursus arctos*), black bear (*U. americanus*), and polar bear (*U. maritimus*). Generally, bears select dens one to 2 km from human activity (roads, habitation, industrial activity) and seemed to tolerate most activities that occurred more than one km from the den. Activity closer than one km and especially within 200 m caused variable responses. Some bears tolerate disturbance even inside the den, but bears will abandon dens in response to activity within this zone, especially early in the denning period. Den abandonment by brown and black bear females with cubs of the year can lead to increased cub mortality. Specific excavated or ground dens are rarely reused, whereas natural caves or hollow trees are reused with varying frequency. There is often some distance between an individual bear's consecutive dens. This indicates that loss of a single denning area following human disturbance will not always lead to deleterious effects, if alternative denning areas are available within the home range.

Key words black bear, brown bear, dens, disturbance, hibernation, physiology, polar bear, *Ursus*

Human activities such as recreation and resource extraction, even when they do not involve direct persecution or habitat degradation, can disturb wildlife (Bromley 1985, McLellan 1990). Responses of mammals to disturbance vary in degree from minor changes in activity pattern to displacement (escape) and reduced reproductive success or survival (Bromley 1985). Some species are able to minimize effects of chronic disturbance by moving away from disturbed areas or limiting use to times when disturbance is absent (Bromley 1985, Mace and Waller 1996). Only if the habitat they are displaced from is limited in availability and critical will other costs, such as increased predation risk or a long-term decrease in foraging efficiency, become significant enough to affect survival and recruitment. However, many animals have certain life stages when they are more vulnerable. Carnivores, for example, tend to be confined to an area around a breeding den during the postpartum period when altrical offspring are developing locomotory skills. Disturbance resulting in displacement at this stage

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of the life cycle could have deleterious effects as a new den site must be found and offspring moved (Chapman 1977, Ballard et al. 1987, Thomson 1992).

For most carnivores, the denning period corresponds with summer conditions and only reproductive animals are affected. Bears (Ursidae) represent an exception. Parturient females and most individuals of other age and sex classes remain seque-stered in dens for up to 6 months when hibernating (Ramsay and Dunbrack 1986). Because of strict energy constraints and the importance of the den structure, disturbance in this phase of the annual cycle may have greater negative affects on survival and reproduction than disturbance at other times of the year.

For many bear populations, potential for human disturbance at winter dens has increased because 1) winter recreation in bear habitats is becoming increasingly popular, 2) extraction industries (logging, mining) are increasing their activity in bear habitat, and 3) bear populations are re-expanding their range into many areas with human activity. Many authors have expressed concern about the impacts of human activity on denning bears (Mannville 1983, Peek et al. 1987, Mattson 1990, Goodrich and Berger 1994, Wiig et al. 1996), and the subject was ranked among the top 5 research needs with respect to military activity (Asherin and Gladwin 1988).

This review summarizes what is known about bear denning chronology, behavior, physiology, and habitat selection and how denning bears respond to specific disturbance stimuli. The review covers 3 species of bears found in temperate and arctic regions, polar bears (*Ursus maritimus*), brown bears (*U. arctos*), and black bears (*U. americanus*).

Chronology of denning: potential for disturbance in time

While hibernation and denning are effective methods to conserve energy during winter, not all bears enter dens (Table 1). Among polar bears, pregnant females are the only class to consistently use dens (Ramsay and Stirling 1988). Other age and sex classes may reduce activity for periods of up to a month and use temporary shelters, but these are not regarded as true dens (Messier et al. 1992, 1994). Most age and sex classes of brown bears enter dens for part of winter. One exception is on Kodiak Island, Alaska, where some males remain active all winter, possibly because of the availability of spawning salmon (*Oncorhynchus* spp., Van Daele et al. 1990). Some male brown bears from southern Europe also remain active during all or part of winter (Clevanger et al. 1992, Huber and Roth 1996, Roth et al. 1996). The variation observed in denning behavior reflects the large geographic area over which black bears are found. All black bears in northern latitudes den for winter, but many males and nonreproductive females remain intermittently or continually active during winter in southern ranges that lack snowfall (Hellgren and Vaughan 1987, Doan-Griber and Hellgren 1996).

Within populations, dates of den entry and exit vary greatly among age and sex classes and years. Adult males den consistently for shorter periods than pregnant females, with other classes having intermediate denning periods (Table 1, Lindzey 1981). In consequence, entry or emergence dates can vary by several months within a population in the same year (LeCount 1983, Van Daele et al. 1990). Annual variation in dates of den entry is generally attributed more to availability of autumn foods (berries, nuts, mast, salmon) than snowfall (Craighead and Craighead 1972, Johnson and Pelton 1980*a*, Tietje and Ruff 1980, Schooley et al. 1994, Van Daele et al. 1990). Emergence dates can vary with spring snowmelt and the consequent risk of dens being flooded (Schoen et al. 1987). Generally, length of time spent in dens is determined by climate and thereby habitat, latitude, and altitude. Bears living in northern areas den for longer periods than their southern counterparts. For example, duration of hibernation for pregnant female black bears can vary from 7 months in Alaska (Smith et al. 1994) to 3 months in Tennessee (Johnson and Pelton 1980*a*).

The period with potential for disturbing denning bears clearly varies with region and year. This period is not just the period of snow cover, as many bears begin denning before snow falls and may emerge before or after snowmelt. Because the denning period appears to be relatively predictable within a given region if snow conditions and autumn food abundance are monitored, there is a possibility of avoiding potentially disturbing activity during the period when bears den. However, hunting in early spring or late autumn, any snow-oriented winter recreation activities, and extraction industries that use frozen ground in winter all have the potential to disturb denning bears.

Table 1. Chronology of denning for polar, brown, and black bears.

Location	Latitude	Who dens? [a]	Denning period[b] Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	Ref.[d]
Polar bears													
Svalbard	78	rF only							oo	oo			1
Canada archipelago	72–76	rF only	oo•o	oo++	++++	++++	++++	++++	ooo•	o			2
Beaufort Sea	68–76	rF only		oooo	oo•o	++++	++++	++++	oooo	•ooo			3
Wrangel Island	72	rF only		?	?				oo•	oo			4
Manitoba	57	rF only		?	?			o	o•oo	o			5
Manitoba	57	rF only		oooo	o+++	++++	++++	+++o	oooo				6
Ontario	55	rf only		?	?			o	•ooo	o			7
Brown bears													
NW Alaska	68	all		ooo•	oooo	++++	++++	++++	++++	++oo	o•o		8
N Sweden	67	all	o	•oo+	++++	++++	++++	++++	++++	++oo	•ooo		9
Central Alaska	62	all	o	o•oo	o+++	++++	++++	++++	++++	+ooo	•ooo	o	10
S Sweden	61	all	o	ooo•	oooo	++++	++++	++++	oooo	o•oo	oooo	o	9
SE Alaska	57	all		oo•	oooo	oo++	++++	++++	+++o	oooo	•ooo		11
NE Kodiak Island	57	not all aM		oo	•ooo	oooo	++++	++++	++oo	oooo	•ooo	oooo	12
SW Kodial Island	57	all		oo	ooo•	oooo	++++	++++	oooo	oooo	•ooo	oooo	12
Banff NP Alberta	52				oo++	++++	++++	++++	+++o	oo			13
NW Montana	48	all			o•o	++++	++++	++++	+++o	o•o			14
NW Montana	48	all		ooo	•ooo	o+++	++++	++++	+ooo	•ooo	oo		15
Croatia	48	not all											16
Yellowstone NP	44	all		o	o•++	++++	++++	++++	++++	oo			17
Yellowstone NP	44	all	o	oooo	o•oo	ooo+	++++	++oo	ooo•	oo			18
N Spain	43						oo			oo			19
N Spain	43					ooo	oo•o	++++	+o•o	oo			21
Abruzzo, Italy	42	not all aM											21
Black bears													
Central Alaska	64	all	oo	•oo+	++++	++++	++++	++++	++++	+oo•			22
Central Alaska	62	all	ooo	o•oo	oo++	++++	++++	++++	++++	+ooo	•oo		23
Kenai, Alaska	60	all	o	oo•o	oo++	++++	++++	++++	+++o	oo•o	oo		23
Central Alberta	55	all		oo•o	o+++	++++	++++	++++	++++	o•o			24
Cental Ontario	55	all	o	ooo•	oooo	++++	++++	++++	+++o	o•oo			25
NW Montana	48	all		oooo	o•oo	++++	++++	++++	+++o	•ooo	o		15
N Minnesota	47	all		•						•			26
N Maine	46	all		ooo	o•o+	++++	++++	++++	++++	ooo•	o		27
Washington	46	all		o	•ooo	++++	++++	++++	o•oo	oo			28
S Montana	45	all	o	oo•o	o+++	++++	++++	++++	++++	o•oo	o		29
N Michigan	45	all			ooo	o•oo	++++	++++	o•oo	oo			30
Idaho	44	all		ooo	•ooo	++++	++++	++++	++++	+o•o			31
New York	42	all			oooo	•ooo	++++	++++	+ooo	•ooo			32
California	38	63% aM act			o	oo•			•	oooo	oooo		33
Nevada	37	all				o•o+	++++	++++	+o•o	o			34
Nevada	37	all			o•	o+++	++++	++++	++oo	•o			34
Virginia	36	14% act				oo•	oo++	++++	++oo	•oo			35
N. Carolina	35	some act				oo•	o+++	++++	+++•	o			36
Arizona	35	all		oo	oo•o	oo++	++++	+++o	oooo	•ooo	o		37
Tennessee	35	all				o	•o++	++++	++oo	•ooo	o		38
E Arkansas	35	5 % act				•o	oo++	++++	++oo	o•			39
E Arkansas	33	all					o•o+	++++	+o•o				40
California	34	no			oooo	o•oo	++++	++++	oo•o	o			41
Louisiana fo[c]	32	34 % act			o	•o++	++++	++++	++++	ooo•	oooo		42
Florida fo	30	all aM act				o•	o+++	++++	++++	+++•	oo		43
N. Mexico fo	29	all aM act				o•	o+++	++++	++++	+o•o			44

[a] "rF" = reproductive female (with yearlings or cubs-of-the-year), "aM" = adult males, "act" = active.

(*continued*)

Table 1 (*continued*). Chronology of denning for polar, brown, and black bears.

[b] Each month is divided into 4 quarters. The quarter containing the average entrance and emergence dates (•), the range of quarters in which bears began to den or emerge (o), and the quarters during which all bears were denned (+) are shown.

[c] Populations where data on females only is presented are marked with "fo".

[d] 1=Larsen 1985, 2=Messier et al. 1994, 3=Armstrup and Gardner 1994, 4=Uspenski and Kistchinski 1972, 5=Jonkel and Cowan 1971, 6=Ramsay and Stirling 1988, 7=Kolenosky and Prevett 1983, 8=Ballard et al. 1991, 9=Swenson unpublished, 10=Miller 1990, 11=Schoen et al. 1987, 12=Van Daele et al. 1990, 13=Vroom et al. 1977, 14=Servheen and Klaver 1983 cited in LeFrance et al. 1997, 15=Aune 1994, 16=Huber and Roth 1996, 17=Craighead and Craighead 1972, 18=Judd et al. 1986, 19=Clevanger and Purroy 1991, 20=Naves and Palomero 1993, 21=Roth et al. 1996, 22=Smith et al. 1994, 23=Schwartz et al. 1987, 24=Tietje and Ruff 1980, 25=Kolenosky and Strathearn 1987, 26=Rogers 1987, 27=Schooley et al. 1994, 28=Lindzey and Meslow 1976, 29=Mack 1990, 30=Manville 1987, 31=Beecham et al. 1983, 32=O'Pezio et al. 1983, 33=Graber 1990, 34=Goodrich and Berger 1994, 35=Hellgren and Vaughan 1989, 36=Hamilton and Marchinton 1980, 37=LeCount 1983, 38=Johnson and Pelton 1980a, 39=Smith 1986, 40=Oli et al. 1997, 41=Novick et al. 1981, 42=Weaver and Pelton 1994, 43=Wooding and Hardisky 1992, 44=Doan-Crider and Hellgren 1996.

Den construction and den-site selection: potential for disturbance in space

Types of dens used and the locations selected varied within and among species (Table 2). Polar bears generally use snow dens (dens tunneled into snowdrifts). Only in the southerly Hudson Bay region did polar bears excavate dens in the soil (Kolenosky and Prevett 1983, Clark et al. 1997). Generally, polar bear dens were located in tundra habitats, although pack ice was used extensively in the Beaufort Sea (Lentfer and Hensel 1980, Armstrup and Gardner 1994) and the tundra-boreal forest ecotone was used around Hudson Bay (Ramsay and Stirling 1990, Clark et al. 1997). Dens on land were commonly concentrated, resulting in locally high densities (Uspenski and Kistchiski 1972, Larsen 1985, Armstrup and Gardner 1994, Clark et al. 1997, Ovsyanikov 1998), although this trend was not universal (Messier et al. 1994). These concentrations often were associated with the upper portion of steep hillsides and lee slopes (Larsen 1985, Ovsyanikov 1998). Dens in the tundra-forest ecotone tended to be more dispersed, although confined generally to specific suitable regions (Clark et al. 1997, Ramsay and Stirling 1990). Successive dens occupied by individual bears tended to be within the same geographic region, but not at the same site, with a mean of 308 km (range 20-1,300 km) between dens. In some regions, annual variation in denning location could be due to shifting ice conditions (Stirling and Andriashek 1992). Dens varied in distance from the sea, with dens on Svalbard (Norway) averaging 3 km and dens around Hudson Bay ranging from 29 to 118 km (Kolenosky and Prevett 1983, Larsen 1985, Ramsay and Andriashek 1986). Pack-ice dens were the most dispersed and least predictable, in part due to the shifting nature of the substrate (Armstrup and Gardner 1994, Lentfer 1975). The nature of snow dens precludes reuse.

Brown bears used a greater variety of den types, with much variation among populations. Excavations in soil, often dug under tree roots or ant hills for stability, were the most common, although natural cavities and caves appeared to be used where they occur, especially in southern European and coastal Alaskan areas. Brown bear dens were associated rarely with hollow trees or were simply dug in snow. Dens in natural cavities were reused at much greater rates than excavated dens, indicating that they were either preferred and more limited or that excavated dens did not persist (Van Daele et al. 1990, Groff et al. 1998). Concentrations of denning brown bears have been found in areas where natural cavities (Naves and Palomero 1993, Huber and Roth 1996) and excavated dens (Swenson et al. 1996) were used. Successive dens for individual bears tended to be within the same region but almost never in the same den structure, with mean distances varying from 1.7 km to 8.8 km in separate studies and with a few individuals moving up to 30 km (Schoen et al. 1987, Miller 1990, Van Daele et al. 1990, Ballard et al. 1991). Females showed greater degrees of den-area fidelity than males (distances separating dens in separate years averaging 3.5 versus 8.8 km in Southeast Alaska, 1.7 versus 7.8 km on Kodiak Island for females and males, respectively). Fidelity to region rather than den also indicated that suitable denning sites are not often limited. Dens were located in treeless alpine areas, the forest-alpine ecotone, or forest depending on availability. There appeared to be a trend for middle elevations to be used, with valley bottoms and high peaks avoided (Table 2). The general pattern was for the use of relatively high-altitude areas with the most stable snow conditions possible, rather than specific habitat types. Use of steep slopes was strong, with mean slopes ranging from 30° to 50°. Aspect use varied enormously within and between studies (Harding 1976, Judd et al. 1986), perhaps

Table 2. Topographic and habitat characteristics (mean and (range)), and den construction type of brown bear and black bear dens.

Location	°N	Slope use in degrees	Altitude used	Altitude available	Den construction (%)[a] N	Exc	Cave	Veg	Sn	Tr	Habitat type (%)[b] n	Tun	For	Eco	Alp	Ref[c]
Brown bears																
N. Yukon	70	40 (20–80)			24	96			4		24	100				1
N. Alaska	70	54	816		29	93	7				29			10	90	2
N. Alaska	70		1,063		49	70	30									3
NW Alaska	68	>30	500	0–1,200	86	100										4
N Alaska	68	(20–35)			52	75	25									5
N Sweden	67				21	47	43		10							47
Central Alaska	62	32 (11–60)	1,200 (320–1,626)		96	99	1				102			48	52	6
SW Yukon	62	35 (30–40)	1,250		10	100										7
S Sweden	61				125	86	10		4							47
SE Alaska	57	35 (5–75)	640 (6–1,190)	0–1,400	38	29	63		8		38		52	22	13	8
Kodiak Island	57	>45	450 (128– 915)	0–1,000	135	82	13		5		320		1	43	56	9
(2 sites)			665 (91–1,189)	0–1,300												
SW Alaska	57	40 (0–60)	450 (30–1,000)	0–1,200	30	96			4		30			50	50	10
Rocky Mts.	53	57	2,174		60	93	7				60			100		11
Rocky Mts	53	26	2,057								24		42	8	50	12
Jasper NP	53	27 (15–40)	2,236		10	90	10									13
Banff NP	53	33 (21–35)	2,200 (2,050–2,300)	1,300–1,500	47	100					38		71	29		14
NW Montana	48	30 (21–35)	2,124 (2,050–2,500)	850–3,000	15	100										15
NW Montana	48	57 (51–62)	2,166	1,280–2,800												16
N. Italy	46	39 (28–60)	1,431 (970–1,940)	500–3,000	21	10	90				19		95		5	17
N. Italy	46	44 (<63)	1,600 (951–2,450)	700–2,300	12	75	25									18
Croatia	46	48 (20–90)	836 (450–1,370)	400–1,500	28	7	79		10	4	28		100			19
Yellowstone NP	44	45 (30–60)	2,470 (2,000–3,050)	1,500–4,200	33	91	6		3		55		100			20
Yellowstone NP	44				11	100										21
N Spain	43		(1,400–1,520)		7		100				7		100			22
N Spain	43	32 (11–52)	1421 (580–2,400)		74	22	78				74		95	5		23
S France	43				11	42	68				11		100			24

(*continued*)

[a] Exc = excavated, Cave = natural cave or cavity, Veg = vegetation only nest, Sn = snow den, Tr = tree or hollow log den,

[b] Tun = tundra / muskeg, For = forest / swamp forest and shrub, Eco = forest / alpine ecotone, Alp = alpine meadows

[c] 1=Harding 1976, 2=Garner et al. 1984, 3=Quimby and Snarski 1974 cited in LeFrance et al. 1987, 4=Ballard et al. 1991, 5=Reynolds et al. 1976, 6=Miller 1990, 7=Russel 1978, 8=Schoen et al. 1987, 9=Van Daele et al. 1990, Smith and Van Daele 1990, 10=Lentfer et al. 1972, 11=Aune et al. 1986, 12=Wielgus 1986 cited in LeFrance et al. 1987, 13=Russell 1978 cited in LeFrance et al. 1987, 14=Vroom et al. 1977, 15=Servheen and Klaver 1983 cited in LeFrance et al. 1987, 16=Aune 1994, 17=Groff et al. 1998, 18=Roth 1972, 19=Huber and Roth 1996, 20=Judd et al. 1986, 20=Craighead and Craighead 1972, 22=Clevanger and Purroy 1991, 23=Naves and Palomero 1993, 24=Camarra 1987, 25=Smith et al. 1994, 26=Schwartz et al. 1987, 26=Tietje and Ruff 1980, 28=Kolenosky and Srathearn 1987, 29=Lindzey and Meslow 1976, 30=Jonkel and Cowan 1971, 31=Manville 1987, 32=Mack 1990, 33=Beecham et al. 1983, 34=Alt and Gruttadauria 1984, 35=Beck 1986, 36=Goodrich and Berger 1994, 37=Hayes and Pelton 1994, 38=Oli et al. 1997, 39=Hellgren and Vaughan 1989, 40=Hamilton and Marchinton 1980, 41=LeCount 1983, 42=Johnson and Pelton 1980b, 43=Wathen et al. 1986, 44=Novick et al. 1981, 45=Weaver and Pelton 1994, 46=Wooding and Hardisky 1992, 47=Doan-Crider and Hellgren, 1996, 48=Swenson unpublished.

due to selection for slopes with the right wind and sun exposure to produce stable snow conditions for the required length of time.

Black bears used a much greater diversity of den types (Table 2) compared to polar or brown bears. Excavated dens and natural cavities are used commonly in northern regions, whereas hollow trees and ground nests constructed in dense vegetation are used commonly in southern regions. Rates of reuse vary from 5-6% to 30-58% for excavated dens (Lindzey and Meslow 1976, Tietje and Roff 1980, Beecham et al. 1983, LeCount 1983, Schwartz et al. 1987) and up to 70-100% for natural cavities (Schwartz et al. 1987). Reuse is rarely by the same bear (Novick et al. 1981). Forest or dense shrub areas were the most commonly used habitats for dens. Many black bear populations live in flat taiga or coastal swamp areas, where slope or altitude selection cannot be displayed. In areas with greater topographic variation, 20-50^0 slopes are generally selected at middle altitudes. In areas where black and brown bears have been studied in sympatry, black bears selected lower altitudes than brown bears (Miller 1990, Aune 1994). Aspect selection was complex, without a clear trend, but it was presumed that the local stability of snow conditions is among the important determinants.

Spatial potential for disturbing denning bears is great, as their choice of habitat is often similar to that of people. In arctic areas, industrial activity tends to concentrate along the coast, therefore leading to potential conflict with denning polar bears (Armstrup 1993, Armstrup and Gardner 1994, Wiig et al. 1996). While much development (road and house construction, hydroelectric development) occurs in valley bottoms and thus avoids prime den areas, ski resorts tend to be built on steep slopes with stable snow conditions, exactly the same conditions that brown and black bears select (Goodrich and Berger 1994). Black bears will generally be more vulnerable to valley-bottom disturbance than brown bears because of their greater use of lower slopes (Miller 1990, Aune 1994). The fact that suitable denning habitat can be identified, from field study or by using GIS maps (Clark et al. 1998), means that important areas with concentrations of sites can be given special consideration when planning activity in winter. If disturbance is unavoidable, the fact that bears usually move several kilometers between successive denning seasons and generally have a low level of den reuse implies that loss of a localized denning area (smaller than individual home ranges) to development should have minimal effects provided suitable alternative habitat is available nearby (within the individuals' home ranges). An exception may occur if the disturbed area contains a high number of natural cavities or hollow trees, where these are favored over excavated dens.

There are reasons to expect that different den types offer different levels of physical protection, thermal insulation, acoustic insulation, and vulnerability to flooding and that these factors should have significant effects on reproduction and vulnerability to disturbance (Smith 1986, Oli et al. 1997, McDonald and Fuller 1998). Despite the fact that this data is essential to evaluate the relative importance of the different den types, there is not enough information yet for definitive conclusions.

Hibernation physiology and the potential energetic costs of disturbance

The occurrence of true hibernation in bears has been debated for over 30 years, but the answer depends on how hibernation is defined (Watts et al. 1981). If the definition is generalized to include significant energy savings through body temperature reduction and a slowing of metabolism, then bears must be regarded as functional hibernators (Folk et al. 1977, Farley and Robbins 1995).

During the denning period, bears decrease core body temperature to between 32°C and 35°C (Hissa 1997, Hellgren 1998). Although smaller hibernating species may allow their body temperatures to drop to close to 0°C, bears appear to have a limit of 32°C (Hissa 1997, Hellgren 1998). Metabolism is reduced and heart rate slows to approximately 18 beats/minute (Reynolds et al. 1986). An energy-sparing sleep state called non-rapid eye movement (NREM) is entered. The structure of the den, any bedding, and the layer of air trapped between bear and den wall provide thermal insulation from winter temperature extremes. Rates of heat flow between the bear and outside are therefore reduced and rates of energy use are reduced by between 60 and 80% (Watts et al 1987, Watts and Jonkel 1988, Watts and Cuyler 1988).

Bears do not eat, drink, defecate, or urinate between den entry and den emergence. Therefore, all energy is provided by fat reserves, water is obtained as a product of fat metabolism, and all metabolic waste products are stored (Folk et al. 1972, Ramsay and Dunbrack 1986, Hissa 1997, Hellgren 1998). Energy requirements of pregnant females are relatively high while denning because they give birth to multiple altrical young in mid-winter and lactate for several months (Ramsay and Dunbrack 1986, Farley and Robbins 1995). Despite the reduced metabolism of the hibernation state,

Table 2 (*continued*). Topographic and habitat characteristics (mean and (range)), and den construction type of brown bear and black bear dens.

Location	°N	Slope use in degrees	Altitude used	Altitude available	Den construction (%)[a]						Habitat type (%)[b]					Ref[c]
					N	Exc	Cave	Veg	Sn	Tr	n	Tun	For	Eco	Alp	
Black bears																
Central Alaska	64			Flat	41	83	5		12		41	100				25
Central Alaska	62	35	624 (267–1,324)	300–2,300	91	56	41			3	91		91	9		26
South Alaska	61	35			17	20	60			20						26
South Alaska	60			Flat	96	96	3			1	96		100			26
Central Alberta	55			Flat	37	95					37		100			27
Central Ontario	53			Flat	98	89	3	3		5	98		100			28
NW Montana	48	28 (20–38)	1,715 (1,632–1,798)	1,280–2,863												16
Washington	46				12	67	16			17						29
Central Montana	46				127	14	72	13								30
N Michigan	45			Flat	31	78		3	19		31		100			31
S. Montana	45	28 (14–37)	2,239 (1,768–2,682)	1670–3000	16	31	69									32
W. Idaho	44	15			65	72	3			25	65		100			33
Pennsylvania	40				27	11	63	22		4						34
Colorado	37				55	35	62	3								35
Nevada	37	15(0 – 35)	2,656 (2,250–3,000)	1,890–3,460	9		56	22		22						36
Nevada	37	21 (10–33)	2,310 (1,799–2,713)	1,560–2,940	30	3	37			60						36
Arkansas	36				48	12	67	17		4	48		100			37
Arkansas	36			Flat	51	4		6		90	51		100			38
Virginia	36			Flat	28	39		50		11	29		100			39
N Carolina	35			Flat	5			80		20	5		100			40
Arizona	35	30 (7–48)	1,500 (750–1,900)	575– 2,300	68	76	24				68		100			41
Tennessee	35				36	28	6			66	36		100			42
Tennessee	35	31	963	230–2,024	95	13	11	7		69						43
S California	34	49 (30–60)	2,250 (1,900–2,500)	1,200–2,750	7	100					7		100			44
Louisiana	32			Flat	32			44		56	32		100			45
N. Florida	30			Flat	14			100			14		100			46
N. Mexico	29				14		100									47

[a] Exc = excavated, Cave = natural cave or cavity, Veg = vegetation only nest, Sn = snow den, Tr = tree or hollow log den,

[b] Tun = tundra / muskeg, For = forest / swamp forest and shrub, Eco = forest / alpine ecotone, Alp = alpine meadows

[c] 1=Harding 1976, 2=Garner et al. 1984, 3=Quimby and Snarski 1974 cited in LeFrance et al. 1987, 4=Ballard et al. 1991, 5=Reynolds et al. 1976, 6=Miller 1990, 7=Russel 1978, 8=Schoen et al. 1987, 9=Van Daele et al. 1990, Smith and Van Daele 1990, 10=Lentfer et al. 1972, 11=Aune et al. 1986, 12=Wielgus 1986 cited in LeFrance et al. 1987, 13=Russell 1978 cited in LeFrance et al. 1987, 14=Vroom et al. 1977, 15=Servheen and Klaver 1983 cited in LeFrance et al. 1987, 16=Aune 1994, 17=Groff et al. 1998, 18=Roth 1972, 19=Huber and Roth 1996, 20=Judd et al. 1986, 20=Craighead and Craighead 1972, 22=Clevanger and Purroy 1991, 23=Naves and Palomero 1993, 24=Camarra 1987, 25=Smith et al. 1994, 26=Schwartz et al. 1987, 26=Tietje and Ruff 1980, 28=Kolenosky and Srathearn 1987, 29=Lindzey and Meslow 1976, 30=Jonkel and Cowan 1971, 31=Manville 1987, 32=Mack 1990, 33=Beecham et al. 1983, 34=Alt and Gruttadauria 1984, 35=Beck 1986, 36=Goodrich and Berger 1994, 37=Hayes and Pelton 1994, 38=Oli et al. 1997, 39=Hellgren and Vaughan 1989, 40=Hamilton and Marchinton 1980, 41=LeCount 1983, 42=Johnson and Pelton 1980b, 43=Wathen et al. 1986, 44=Novick et al. 1981, 45=Weaver and Pelton 1994, 46=Wooding and Hardisky 1992, 47=Doan-Crider and Hellgren, 1996, 48=Swenson unpublished.

weight loss during winter can be substantial. Weight losses of 8-20% have been reported for nonreproductive animals and from 25 to 40% for reproductive females (Tietje and Ruff 1980, Watts et al. 1981, Kingsley et al. 1983, Watts 1990, Farley and Robbins 1995) and appear to be more pronounced for brown bears than black bears (Farley and Robbins 1995). Clearly there is a limited margin of energy available for bears to compensate for increased energetic expenditure due to disturbance while denning.

In general, little is known about the physiological responses of denning bears to disturbances and their energetic costs, but there are enough indications and a sufficient understanding of the behavioral and physiological processes to make predictions. Potential responses to disturbance range along a continuum. First-level responses could involve waking from NREM sleep, slight body warming, or increased heart rate. These are followed by movement within the den, raising body temperature to normal levels with an accompanying 60-80% increase in metabolic rate, and ultimately den abandonment. Based on the data reviewed here, we predict that the impact of these responses on survival increases dramatically at each step, with den abandonment having the greatest cost, especially for neonatal cubs, which may not survive exposure to ambient temperature during midwinter (Blix and Lentfer 1979). However, even minor physiological changes like frequent waking or small increases in body temperature may have a cumulative effect on energy use and consequent weight loss that may be significant.

Unlike small mammalian hibernators, bears can wake and achieve relatively full mobility over a matter of minutes (Nelson and Beck 1984). Observations indicate that experimental bears are sensitive to sounds and may change physiological state in response to minor acoustic stimuli (B. Barnes, personal observation), although no experimental work is known which specifically tested these responses. The period required to regain their previous quiescent, hibernating state may vary from a few days to over a week (Craighead et al. 1976).

How do denning bears respond to disturbance?

No systematic data are available on how denning bears react to disturbance using controlled stimuli. The only response that has been generally reported is den abandonment, which is the most extreme reaction possible. Here we review the available information and try to derive some patterns from it.

Reynolds et al. (1986) presented data on heart rate and activity responses of 3 brown bears exposed to human activity (seismic exploration). Results were varied, but in 3 of 5 cases, bears responded to seismic shots, drilling, or a vehicle driving at a distance of one to 2 km with increased heart rate or increased physical activity. A snow-tractor driving within 100 m of the den had no effect on one bear. Other studies have reported increased activity of denned bears indicated by motion-sensitive radio-collars in response to radio-

Table 3. Linear mean distances (with range) of bear dens to various centers of human activity.

	Distance[a] to human activity[b] km				
Region	Path	Road	Habitation	Activity	Reference
Brown Bear					
Yellowstone		0.5 (0.1–1.5)	1.5 (0.2–4.0)		Craighead & Craighead 1972
Italy	0.2(0.1-0.5)	1.2 (0.4–2.8)	3.5 (1.3–6.5)		Groff et al. 1998
Spain		1.7	2.0		Naves & Palomero 1993
Croatia		0.5 (0.1–1.6)	1.4 (0.2–4.0)		Huber & Roth 1996
SW Alaska				≥1.5	Smith & Van Daele 1990
Black Bear					
Nevada		≥0.8			Goodrich & Berger 1994
Alberta		≥0.3		≥1.5	Tietje & Ruff 1983
Michigan				1.0(0.1–2.7)	Manville 1987
SE Alaska				≥3.4	Schoen et al. 1987

[a] Distances do not account for differences in altitude, which in some cases may be significant. In several cases the distance presented does not represent the mean or the range, but is based on a minimum distance that some bears were observed to den from human activity areas.

[b] Path = a nonvehicle pedestrian path, road = vehicle use, habitation = house, village or town, activity = industrial activity and other unspecified point sites with human presence in winter.

tracking overflights (Schoen et al. 1987, Smith and Van Daele 1990).

Further indications of bear response to disturbance are available from the distances of dens from human features like roads, towns, and industrial sites (Table 3). The presence of bear dens within one kilometer of regularly traveled roads or areas of active human habitation indicates that bears do not totally avoid denning in areas purely because of their proximity to human activity (Tietje and Ruff 1983). A large black bear population denned within an extensive military training area (Fort Wainwright, Alaska) without any registered cases of disturbance by military activity (Hechtel 1991; Smith et al. 1994; M. E. Smith, personal communication). Although Schoen et al. (1987) reported that brown bears gradually withdrew their den sites from an area of developing mining activity in Alaska, the short distances reported for European brown bears were to long-established sources of potential disturbance. In general, bears often appeared to choose dens close (within one km) to fixed sources of predictable disturbance (Smith and Van Daele 1990, McDonald and Fuller 1998). In a sparsely populated area of southern Sweden, brown bears were shown to prefer den sites more than one km from roads and houses and >3 km from villages (Swenson et al. 1996).

Armstrup (1993) and Armstrup and Gardner (1994) present data on polar bear response to disturbance. Denned polar bears appeared to be very tolerant to disturbance close to dens, although when disturbed, they where more prone to leave dens earlier in the season. After they gave birth, the cost of den relocation rises dramatically, as young cubs will be exposed to thermal stress and predation before they are fully mobile. Therefore, females with cubs should tolerate greater levels of disturbance without abandoning dens. Oil-field activity, snow vehicles, and aircraft were tolerated to within 500 m of dens without abandonment. Some approaches <250 m of a few dens caused abandonment, although there was no overall difference between the abandonment rates of disturbed and nondisturbed bears. Two bears were approached to <50 m by snowscooters without effect. This variation could result from how different sounds or vibrations are transferred through snow to the denning bear, as snow dens provide excellent acoustic insulation (Blix and Lentfer 1992). The stress of prepartum recapture inside the den and subsequent relocation of den site did not appear to have any dramatic effects on litter size or spring weight of cubs (Ramsay and Stirling, 1986).

Brown bears showed a similar tolerance for industrial activity disturbance within a few kilometers of dens (Harding and Nagy 1980, Schoen et al. 1987, Smith and Van Daele 1990). Dens that were approached directly were sometimes abandoned (Harding and Nagy 1980, Reynolds et al. 1986, Huber and Roth 1996). Craighead and Craighead (1972) dug into a den, photographed the occupant, and retreated without the bear abandoning the den. Den abandonment also may result from natural circumstances such as flooding (Schoen et al. 1987, Huber and Roth 1996, Oli et al. 1997).

Swenson et al. (1997) found that in Sweden, 9% of brown bears (194 bear winters) abandoned or changed their dens during winter, with no differences between males and females. Adult females with cubs of the year that abandoned dens during winter had significantly greater mortality among their cubs than those that did not abandon their dens (60% versus 6% lost at least one cub). In 18 cases of den abandonment that were investigated on the ground, 12 showed evidence of human activity close by. These activities included hunters (4), forest workers (2), dog tracks (1), digging machine (1), and "people" (4, Swenson et al. 1997). New dens were found within a mean of 5.1 km (range 0.1-30 km) from the former den. In Norway in April 1996, an unmarked female with cubs of the year abandoned her den after being disturbed by a skier and dog looking inside the den. These cubs were abandoned and were humanely killed after several days.

Black bears also abandon dens through natural causes (Hamilton and Marchinton 1980, LeCount 1983, Schwartz et al. 1987, Smith 1986, Mack 1990, Oli et al. 1997). Flooding has been shown to cause cub mortality (Alt 1984); however, the greatest proportion of den abandonments were caused by human disturbance, especially researcher activity. Black bears in dens are often approached on foot to determine den structure and reproductive state and are often weighed and recollared in dens as part of standard field protocols. While some individuals tolerate approach and handling (Doan-Griber and Hellgren 1996) and even weighing and collaring of cubs (Elowe and Dodge 1989) without abandoning their den, others do abandon the den (Table 4). This has led to the abandonment of newborn cubs (Graber 1990, Goodrich and Berger 1994). Black bears that changed dens during winter had a

Table 4. Studies of black bears that report den abandonment (abnd.) from various human-induced causes.

Region	Bear response to disturbance	Reference
Alaska	3 cases of abnd. after den visit	Schwartz et al. 1987
Alberta	6 of 109 den visits caused abnd.	Tietje and Ruff 1980
Ontario	19 of 97 den visits caused abnd.	Kolenosky and Strathearn 1987
Michigan	22 of 45 den visits caused abnd. 2 cases of abnd. following mechanical activity within 200m	Manville 1983 Manville 1987
Montana	3 of 26 bears abnd. during winter following human activity	Mack 1990
Minnesota	2 litters died following female abandonment caused by nonresearch, human disturbance	Elowe and Dodge 1989
Minnesota & Massachussetts	Den visits led to abandonment and cub mortality (unspecified percentage)	Macdonald and Fuller 1998
Idaho	11 of 19 den visits caused abnd. early in season	Beecham et al. 1983
California	8 of 63 den visits caused abnd.	Graber 1990
Nevada	12 of 36 den visits caused abnd.	Goodrich and Berger 1994
N. Carolina	10 of 14 den visits caused abnd.	Hellgren and Vaughan 1989
N. Carolina	1 cases of abnd. after researcher approach 1 case of hunting dogs driving bear from den	Hamilton and Marchinton 1980 Hamilton and Marchinton 1980
N. Carolina	8 of 11 bears abnd. dens due to disturbance	Lombardo 1990
Arkansas	9 of 36 den visits caused abnd.	Smith 1986

greater weight loss than undisturbed bears (25% weight loss versus 16%,Tietje and Ruff 1980). Bears appeared more likely to abandon dens when disturbed early in the season (Tietje and Ruff 1980, Smith 1986, Kolenosky and Strathearn 1987) than later. Southern bears appeared to abandon dens at greater frequency than northern bears (Table 4, but see Doan-Griber and Hellgren 1996 for an exception). Milder winter climates clearly impose a smaller cost of abandonment, thereby implying that bears vary their threshold to disturbance depending on costs. Thresholds varied, but often a cautious human approach (<100 m) to the den was enough to make some bears leave (Manville 1983, Graber 1990, Goodrich and Berger 1994). Smith (1986) found different thresholds for different den types, with tree-denning bears being more tolerant of approach than ground-nesting bears. Other documented sources of disturbance leading to abandonment have included military training (Lombardo 1990), hunting dogs (Hamilton and Marchinton 1980), snowscooter traffic (Elowe and Dodge 1989), and oil-well activity within 200 m of the den (Manville 1987). Most disturbed bears redenned (Kolenosky and Strathearn 1987, Hellgren and Vaughan 1989) and even successfully had cubs (Smith 1986), although this trend was not universal, as some cubs died following den abandonment (Elowe and Dodge 1989, Goodrich and Berger 1994).

In conclusion, there appears to be a pattern that bears readily den within one to 2 km of human activity (roads, habitation, industrial activity) and appear to be undisturbed by most activities that occur at distances greater than one km. Activity closer than one km and especially within 200 m has variable results, with some bears tolerating activity right up to the den. However, there is a significant risk that activity within this zone will lead to abandonment, especially early in the denning season. Den abandonment has been shown to cause cub mortality in black and brown bears. The fact that dens are rarely reused (cavities and tree dens excepted) and that bears usually separate consecutive dens by several kilometers implies that loss of an area to disturbance will not have a great effect, provided that other suitable areas exist nearby.

Recommendations and research needs

Based on this review and analysis, we recommend the following regarding human activity and bear denning:

1) Den concentrations should be identified;

2) den trees or natural cavities should be protected;

3) winter activity should be minimized in suitable or traditional denning areas;

4) if winter activity is unavoidable, it should

begin around the time bears naturally enter dens, so that they can choose to avoid disturbed areas;

5) winter activity should be confined to regular routes as much as possible; valley-floor activity should generally have less effect than valley-slope activity;

6) activity should avoid known bear dens by at least one km;

7) the slightest degree of off-road activity is likely to cause greater effects than any degree of fixed-point or predictable-route activity and should therefore be minimized;

8) tagging cubs in dens may lead to extra mortality and should be avoided in small or endangered populations.

These conclusions are tentative. Controlled disturbances and experiments are required to further determine 1) thresholds that bears have to different stimuli, 2) how bears behaviorally respond to stimuli, and 3) what the costs are in terms of increased metabolism. Because of the endangered nature of many bear populations, such experiments should be conducted on captive bears or on large populations. Furthermore, experiments on the thermal and acoustic properties of different den types are required, as is an extended analysis of existing data on the reproductive effects of den type.

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