ECOLOGY AND POPULATION DYNAMICS OF BLACK BEARS IN MINNESOTA

David L. Garshelis, Andrew Tri, Spencer J. Rettler[1], and Brian J. Dirks[2]

SUMMARY OF FINDINGS

During April 2019–March 2020, we monitored 34 American black bears (*Ursus americanus)* previously radiocollared (mostly with GPS collars) at 4 study sites representing contrasting portions of the bear's geographic range in Minnesota: Voyageurs National Park (VNP, northern extreme, poorest food), Chippewa National Forest (CNF; central), Camp Ripley Training Center (southern fringe), and a site at the northwestern (NW) edge of the range. This is part of an ongoing study, initiated in 1981, with current efforts aimed at causes of mortality and spatial and temporal variation in cub production. During summer, we captured and collared 11 more bears in the CNF. Hunting has been the primary source of mortality in all areas; even though VNP and Camp Ripley are unhunted, bears may wander off to other areas in fall where they are vulnerable to hunters. Hunters were asked not to shoot collared bears, all of which are conspicuously marked with large colorful eartags. Two were shot in the CNF this year. Reproduction was strongly affected by food supply. Bears grew fastest and matured earliest in the NW and Camp Ripley. Age of primiparity was most delayed in VNP. Litter size, though, did not correspond with weight. Food supply in the CNF has significantly diminished since the study began there in the 1980s, but there is no indication of reduced reproduction, indicating that these bears compensated for the reduced natural foods through changes in behavior (e.g., enlarged home range size, altered habitat use, increased use of human-related foods — all the subject of a companion study).

INTRODUCTION

Telemetry-based research on American black bears (*Ursus americanus)* was initiated by the Minnesota Department of Natural Resources (MNDNR) in 1981, and has been ongoing continuously since then. For the first 10 years, the bear study was limited to a site near the geographic center of the Minnesota bear range, in an area mainly within or abutting the Chippewa National Forest (CNF; Figure 1). The CNF is one of the most heavily hunted areas of the state, with large, easily-accessible tracts of public (national, state, and county) forests. A chief goal at that time was to assess causes of mortality, specifically the relative impacts of hunting. This study began just as the MNDNR switched from an unrestricted bear hunt to a quota on bear hunting license sales in 1982, in reaction to a concern that the population was being over-hunted. We used black radiocollars and inconspicuous eartags, and requested that hunters treat study bears as they would any other bear.

[1] Department of Fisheries, Wildlife and Conservation Biology, University of Minnesota, St. Paul.
[2] MNDNR Division of Ecological and Water Resources, Camp Ripley, Little Falls, MN.

Commensurately, we studied the reproductive rate, and factors influencing that rate (Noyce and Garshelis 1994). The view among bear biologists at that time was that black bears had one of the lowest reproductive rates of any large mammal in North America. But, we found higher rates of reproduction in Minnesota than studies in western states.

Using physical mark–recapture, where collared bears were the marked population, we tracked an increase in the study population on the CNF through the 1980s, despite harvest rates often exceeding 20% (Garshelis 1991, Garshelis et al. 1988). We found no other factor that significantly affected the population size or trend. A striking finding was that bears rarely died of natural causes. For example, despite (or because of) being in winter dens for 6 months per year, winter weather conditions had no effect on their survival (Garshelis et al. 2020).

We also gained considerable new information about the ecology of bears. Notable findings included: a flexible diet, but with conspicuous effects of food supply on rates of mortality (from hunting: Noyce and Garshelis 1997) and reproduction; varied use of habitat that reflected the changing availability of foods during the course of the year and among years, as well as bears apparently striving for dietary diversity (Garshelis and Noyce 2008); extensive seasonal movements (migrations) to take advantage of richer food sources outside their normal home ranges (Noyce and Garshelis 2011, 2014); and diverse sites and structures used as den sites, which showed no relation to reproduction or survival (Garshelis et al. 2020).

To better understand the dynamics of bear populations across Minnesota, we added more study sites, including 2 sites where bear hunting was prohibited, and 1 site at the front of a recent geographic expansion, where the habitat was dominated by agriculture. We hypothesized that causes of mortality and rates of reproduction would differ among these sites.

OBJECTIVES

1. Compare sources of bear mortality in different parts of the bear range.
2. Quantify temporal and spatial variation in cub production and survival.

STUDY SITES

During the 1980s, the CNF study site was heavily logged, resulting in a matrix of stands of various ages, with many small unpaved logging roads. A unique feature of this study site is that the east side is dominated by upland forests, largely aspen (*Populus tremuloides, P. grandidentata*), whereas a large swath of the western part of this area is a forested bog dominated by black spruce (*Picea marina*) and tamarack (*Larix laricina*). In recent years, more roads have been paved and/or widened; also, forest cutting on federal lands has diminished, so forests have aged and the amount of aspen on the landscape has declined. Nearly all bear foods are found in the understory. Oaks (*Quercus* sp.) are not common anywhere in this area, and commercial agriculture is nonexistent. A series of population estimates for this study site indicate that it increased through the 1980s, but diminished by at least half by 2012 (Garshelis 1991, Garshelis and Noyce 2013, Gondek et al. 2016).

In 1991 our study expanded to include Camp Ripley Training Center, a National Guard facility at the southern periphery of the primary bear range (Figure 1). Bear hunting is prohibited on Camp Ripley, but bears may be hunted if they range outside. Oaks are plentiful, which accounts for bears growing much faster and to a larger mature size than in the CNF (Figure 1). The 210-km^2 area is long and narrow (6–10 km wide), and bordered by highways and cornfields.

In 1997 we added Voyageurs National Park (VNP), located along the northern edge of the Minnesota bear range (bordering Canada; Figure 1). The study site is a 300-km^2 roadless peninsula bounded by 3 large lakes. VNP had the poorest and shallowest soils, no timber cutting, and a largely coniferous forest, so provided the least food for bears. Bears in this area grew slowly and never reached the size of CNF bears (Figure 1). Hunting is prohibited, but bears are exposed to hunting if they leave the park.

In 2007, we initiated work at the northwestern edge of Minnesota's bear range (NW; Figure 1). This area is largely agricultural, although only 2% of the land area is planted with crops consumed by bears. Forested land, which comprises less than 20% of the area, is patchily distributed in small, privately-owned woodlots and state Wildlife Management Areas, which are open to hunting. The density of roads is high. A low density of bears occupied this area until 1995, when poor natural food in neighboring areas spurred an influx of bears attracted to corn and sunflowers. Since then the density of bears in this area has remained higher. Despite the patchy habitat, bears in this area grew quickly and attained adult sizes similar to Camp Ripley bears (Figure 1), due to rich natural foods and agricultural crops (Ditmer et al. 2016, 2018).

METHODS

During May−August, 2019, we captured bears in the CNF with barrel traps or Aldrich foot snares, and immobilized them with a relatively new drug for use in black bears called BAM (commercial drug combination of butorphanol, azaperone, and medetomidine; ZooPharm, Fort Collins, Colorado), as per Williamson et al. (2018). During December–March, we visited all radiocollared bears once or twice at their den site and immobilized them with Telazol. For all handling, we measured and weighed bears, assessed body condition, took blood and hair samples, and extracted a vestigial first premolar to estimate age on all bears whose age was unknown (i.e., first handling of bears older than cubs). We changed or refit the collar, as necessary. We collared bears that we thought would not disperse from the study area. We used GPS-Iridium collars (Telonics Inc., Mesa, AZ) on all but yearlings in the CNF, and mainly very high frequency (VHF) collars on the other study sites. All collared bears had brightly-colored, cattle-size ear tags (7x6 cm; Dalton Ltd., UK) that would be plainly visible to hunters. Licensed hunters could legally shoot collared bears, although they were asked not to. Prior to the hunting season (1 September–mid-October), hunters were mailed a letter requesting that they not shoot collared bears with large ear tags, and this request was also made through news releases. Requests to hunters to voluntarily not shoot collared bears have been made through the news media and MNDNR hunting regulations and website since 2001.

We assessed reproduction by observing cubs in March dens. We sexed and weighed cubs without drugging them. We quantified cub mortality by examining dens of radiocollared mothers the following year; cubs that were not present as yearlings were presumed to have died.

RESULTS AND DISCUSSION

Radiocollaring and Monitoring

As of April 2019, the start of the current year's work, we were monitoring 34 radiocollared bears: 22 in the CNF, 8 at Camp Ripley, 2 in VNP, and 2 in the NW (Table 1). During May–August we captured 17 bears in the CNF and collared 11 of them (6M, 5F).

The sex ratio of our sample in the CNF had been heavily skewed toward males; during 2015–2018 we captured 37 males and 10 females (and radiocollared larger males and all females). This year we captured 4 new adult females (all aged 7 or 8 years old). Presumably, these female bears were all living in the study area where we previously trapped, but avoided capture.

Moreover, we did not previously detect them on camera traps. This year we switched bait, from bacon (our traditional bait since the 1980s) to trail mix (nuts, dried fruit, small bits of chocolate). It is unclear whether this was particularly attractive to these bears. We stopped using bacon because it decomposed in just a few days and needed to be constantly changed.

Mortality

Since 1981, we recorded the cause of death for 391 radiocollared bears, 76% of which died (or likely died) from legal hunting (Table 2). During the 2019 bear hunting season, 2 collared CNF bears were shot (Table 1). In all 4 study sites, legal hunting was the primary cause of mortality (Figure 2), despite (a) Camp Ripley and VNP being unhunted (but bears wander outside during fall on foraging trips), and (b) hunters being asked to not shoot collared bears with large ear tags for the past 19 years (spanning the full period of the NW study).

Vehicle collisions and killing of nuisance bears each represented 7% of the pooled mortality that we observed within these 4 study sites (Table 2). One CNF collared adult male was killed as a nuisance this year, supposedly mistaken as a raccoon (*Procyon lotor*) in the trash. No collared bears were killed on roads this year. Vehicle collisions have been most common at Camp Ripley (Figure 2), which is flanked by 2 highways with fast-moving traffic.

Natural mortality accounted for <5% of deaths of collared bears, aged 1–39 years. When we established the 4 study sites we hypothesized that natural mortality would be highest in VNP, since inside the park there is no legal hunting, no roads, and no killing of nuisance bears. This year, 1 of 2 females (6-year old sisters who we have been monitoring to assess age of first reproduction) died apparently from wolf predation while in her den. We only found a chewed collar on top of the snow in mid-March and never found the den site, so we were unable to know for sure what happened. Interestingly, though, this bear chose an open nest den the previous year whereas her sister (who produced her first litter of cubs this year, see below) denned in rock caves for the past 2 years. This is the second wolf-killed collared bear in 2 years; last year wolves killed a collared bear in the NW.

Reproduction

Since 1982, within the 4 study areas, we collected data on 328 litters with 854 cubs. This year we obtained data on 14 new cub litters and 5 yearling litters. This year, like a number of other recent years, we were unable to obtain reproductive data from all of the female dens in Camp Ripley, either because they were too far inside culverts or denned in an area that was off limits to us (impact zone).

Across all years and study sites, litter size averaged 2.6 cubs. Means within study areas ranged from 2.3–2.8; Tables 3–6). In CNF and NW, 3-cub litters were most common (Figure 3). In VNP, where adult females were smaller (Figure 1), 2-cub litters were most common. In Camp Ripley, 3-year-old first-time mothers tended to have 2-cub litters; excluding these, an equal number had 2- and 3-cub litters (Figure 3). We cannot explain why Camp Ripley bears, which are generally heavier than CNF bears (Figure 1), tended to produce smaller litters. NW bears, which were similar in size to Camp Ripley bears, produced mainly 3-cub litters, but also the highest proportion of 4-cub litters (Figure 3).

Sex ratio of cubs in March dens was 50.7% male overall (Tables 3–6). Over the 39 years of monitoring in the CNF, the cumulative cub sex ratio has remained at about 52% male (with yearly variation due to small sample sizes, Table 3). The sex ratio among yearlings in winter dens was more female-skewed (48.2% male), due to a significantly higher mortality among male cubs (23.4%) than female cubs (15.3%; X^2=6.29, P=0.01). Cub mortality was highest in VNP (Table 6), but the 4 sites were not appreciably different.

Age of first reproduction was the reproductive parameter that varied most among study sites. Half the females in Camp Ripley and NW sites produced their first surviving litter at 3 years old, whereas only 3 of 92 (3%) CNF bears had cubs at 3, and no VNP bears produced cubs at 3 or even 4 (Figure 4). Those bears that produced surviving litters at 3 years old had yearlings at 4, so were not available to have cubs again until age 5. Thus, for Camp Ripley and NW bears, only half the bears were available to produce at 4, and 45% did so, leaving only ≈5% that eventually reproduced for the first time at 5. In CNF, only 33% produced at 4 and 40% produced at 5 (only a few of which had also produced at 3). By age 6, about half the bears in each site were producing cubs every year. Two bears currently in our study, both at Camp Ripley, produced cubs at 20 years old (1 this year, 1 last year). Previously, a female in VNP produced cubs at 21 and a female in CNF produced at 22, but both were lost from the study before they reached reproductive senescence. Another female in CNF produced her last litter at 25 years old, and lived until 39.

A few bears occasionally missed having cubs in a year where they were available to do so, extending the litter interval to 3 years (Table 7). This was most common in Camp Ripley, an unexpected finding given that female bears in this area tended to be large. Whereas the small size of bears in VNP resulted in smaller litters and possibly higher cub mortality, it did not cause more missed litters.

Weights of female bears is a major driver of reproduction, as demonstrated by the differences among study sites. Likewise, we found that within the CNF study site, heavier bears were more prolific (Noyce and Garshelis 1994, Garshelis and Noyce 2008). In a companion study in the CNF, Rettler (2018) found that biomass of natural foods was 70% less in the 2010s than what it had been in the 1980s, when we first began working at this site. We have a small sample of collared females in the 2010s, but data so far show no indication of diminished weights or reproduction. In fact, reproductive rates (cubs/adult females monitored), which combine all aspects of reproduction (litter size, litter interval, and age of primiparity) have been higher during the 2010s than during the 1980s and 1990s (Figure 5). To some extent this may be a peculiarity of the relatively small sample size: during 2011–2015 we monitored only the same 2 adult females, each of which produced litters of 3 or 4 cubs every other year. During 2016–2020 we observed 13 different adult females in dens, but 4 were observed for just a single year (2020) when they happened to have had cubs. If all of the currently collared CNF females were monitored another year and remained on a 2-year reproductive schedule, and the 2021 data combined with the 2016–2020 period, the reproductive rate would drop from 0.83 female cubs/adult female to 0.67, which is still above the long-term average from pre-2000 (0.56, Figure 5). Our main conclusion, therefore, is that reproduction showed no indication of a decline despite the drastically reduced abundance of natural foods in the CNF.

Removal of Collars

This study was a part of a larger investigation into how bears in the CNF coped with diminished natural foods. Given that their reproduction appeared not to be negatively affected, we posited that they may have used larger home ranges (see Rettler et al. 2020), used different habitats within their home ranges, and (or) relied more on human-related foods. GPS-collared bears of both sexes were used to test these hypotheses during 2016–2019. With sufficient data now collected, and most collars soon to expire, we terminated data collection on males and non-reproductive females, and removed 19 collars from the CNF sample during this year's winter den work. Also, with sufficient data collected in the NW, we removed collars on the 2 adult females there. Reproductive monitoring will continue with 8 adult female bears in each of the CNF and Camp Ripley, and 1 at VNP (collar kept on because this was her first litter).

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Table 1. Fates of radiocollared black bears in Chippewa National Forest (CNF), Camp Ripley, Voyageurs National Park (VNP), and northwestern Minnesota (NW) study sites, April 2019−March 2020.

	CNF	Camp Ripley	VNP	NW
Collared sample April 2018	22	8	2	2
Trapped and collared	11			
Collared in den				
Killed in vehicle collision				
Killed by Minnesota hunter[a]	2			
Killed as nuisance	1			
Natural mortality			1[b]	
Removed radiocollar	19[c]			2
Dropped radiocollar	2[d]			
Collared sample April 2019	9[e]	8	1	0

[a] Hunters were asked not to shoot collared bears (although it was still legal).
[b] Adult female apparently killed by wolves while denning.
[c] Collars were removed on males and young females.
[d] Expandable collars on 2 yearlings expanded too much and dropped off.
[e] Includes 1 male whose collar was not removed because his den could not be located.

Table 2. Causes of mortality of radiocollared black bears ≥1 year old in 4 Minnesota study sites, 1981–2019. Bears did not necessarily die in the area where they usually lived (e.g., hunting was not permitted within Camp Ripley or VNP, but bears were killed by hunters when they traveled outside these areas).

	CNF	Camp Ripley	VNP	NW	All combined
Shot by hunter[a]	239	13	16	14	282
Likely shot by hunter[b]	9	1	0	4	14
Shot as nuisance	23	2	1	3	29
Vehicle collision	14	10	1	3	28
Other human-caused death	9	1	0	0	10
Natural mortality	8[c]	3	6	1	18[c]
Died from unknown causes	5	2	0	3	10
Total deaths	307	32	24	28	391

[a] Since 2001, the MNDNR has asked hunters not to shoot collared bears, so the proportion killed due to this cause is no longer representative of the population at large.
[b] Lost track of during the bear hunting season, or collar seemingly removed by a hunter.
[c] Only 1 bear died of “old age”.

Table 3. Black bear cubs examined in dens of radiocollared mothers in or near the Chippewa National Forest, Minnesota, during March, 1982–2020. High hunting mortality of radiocollared bears severely reduced the sample size in recent years.

Year	Litters checked	Number of cubs	Mean cubs/litter	% Male cubs	Mortality after 1 year[a]
1982	4	12	3.0	67%	25%
1983	7	17	2.4	65%	15%
1984	6	16	2.7	80%	0%
1985	9	22	2.4	38%	31%
1986	11	27	2.5	48%	17%
1987	5	15	3.0	40%	8%
1988	15	37	2.5	65%	10%
1989	9	22	2.4	59%	0%
1990	10	23	2.3	52%	20%
1991	8	20	2.5	45%	25%
1992	10	25	2.5	48%	25%
1993	9	23	2.6	57%	19%
1994	7	17	2.4	41%	29%
1995	13	38	2.9	47%	14%
1996	5	12	2.4	25%	25%
1997	9	27	3.0	48%	23%
1998	2	6	3.0	67%	0%
1999	7	15	2.1	47%	9%
2000	2	6	3.0	50%	17%
2001	5	17	3.4	76%	15%
2002	0	0	—	—	—
2003	4	9	2.3	22%	0%
2004	5	13	2.6	46%	33%
2005	6	18	3.0	33%	28%
2006	2	6	3.0	83%	33%
2007	2	6	3.0	67%	17%
2008	1	3	3.0	100%	33%
2009	1	3	3.0	33%	33%
2010	1	4	4.0	100%	50%
2011	1	4	4.0	25%	50%
2012	1	3	3.0	67%	33%
2013	1	3	3.0	67%	0%
2014	1	3	3.0	67%	—
2015	0	0	—	—	—
2016	0	0	—	—	—
2017	1	3	3.0	—	0%
2018	4	12	3.0	42%	0%
2019	1	4	4.0	50%	75%[b]
2020	6	22	3.7	50%	—
Overall	191	513	2.7	52%	19%

[a] Cubs that were absent from their mother's den as yearlings were considered dead.
[b] 3 of 4 cubs in 1 litter did not survive.

Table 4. Black bear cubs examined in dens in northwestern Minnesota during March, 2007–2020.

Year	Litters checked	Number of cubs	Mean cubs/litter	% Male cubs	Mortality after 1 year
2007	2	6	3.0	33%	100%
2008	5	15	3.0	67%	22%
2009	1	3	3.0	33%	33%
2010	6	17	2.8	41%	13%
2011	2	4	2.0	75%	25%
2012	4	10	2.5	60%	10%
2013	3	9	3.0	67%	18%
2014	3	8	2.7	0%	33%
2015	2	5	2.5	60%	0%
2016	2	6	3.0	50%	0%
2017	1	3	3.0	0%	0%
2018	1	4	4.0	50%	25%
2019	1	2	2.0	50%	0%
2020	1	4	4.0	50%	
Overall	34	96	2.8	44%	16%[a]

[a] Excludes the total loss of a 5-cub litter in 2007 (which was not within the designated study area).

Table 5. Black bear cubs examined in dens in or near Camp Ripley Training Center, Minnesota, during March, 1992–2020.

Year	Litters checked	Number of cubs	Mean cubs/litter	% Male cubs	Mortality after 1 year[a]
1992	1	3	3.0	67%	0%
1993	3	7	2.3	57%	43%
1994	1	1	1.0	100%	—
1995	1	2	2.0	50%	0%
1996	0	0	—	—	—
1997	1	3	3.0	100%	33%
1998	0	0	—	—	—
1999	2	5	2.5	60%	20%
2000	1	2	2.0	0%	0%
2001	1	3	3.0	0%	33%
2002	0	0	—	—	—
2003	3	8	2.7	63%	33%
2004	1	2	2.0	50%	—
2005	3	6	2.0	33%	33%
2006	2	5	2.5	60%	—
2007	3	7	2.3	43%	0%
2008	2	5	2.5	60%	0%
2009	3	7	2.3	29%	29%
2010	2	4	2.0	75%	25%
2011	3	8	2.7	50%	25%
2012	1	2	2.0	100%	0%
2013	6	14	2.3	50%	21%
2014	1[b]	—[b]	—	—	—
2015	6	15	2.5	20%	10%
2016	0	0	—	—	—
2017	4	10	2.5	60%	0%
2018	2	5	2.5	20%	—[c]
2019	3	7	2.3	71%	0%
2020	3	6	2.0	83%	
Overall	58	137	2.4	50%	17%

[a] Blanks indicate no cubs were born to collared females or collared mothers died before the subsequent den visit to assess cub survival.
[b] Cubs heard, litter not handled. Camera set outside den indicated that all cubs died. This litter not included in total.
[c] No yearling dens could be checked: all were in culverts or in impact area.

Table 6. Black bear cubs examined in dens in Voyageurs National Park, Minnesota, during March, 1999–2020. All adult collared females were killed by hunters in fall 2007, so sample sizes greatly diminished afterward.

Year	Litters checked	Number of cubs	Mean cubs/litter	% Male cubs	Mortality after 1 year[a]
1999	5	8	1.6	63%	20%
2000	2	5	2.5	60%	80%
2001	3	4	1.3	50%	75%
2002	0		—	—	—
2003	5	13	2.6	54%	8%
2004	0		—	—	—
2005	5	13	2.6	46%	20%
2006	1	2	2.0	50%	0%
2007	3	9	3.0	44%	—
2008	0		—		—
2009	0		—		—
2010	1	2	2.0	50%	0%
2011	1	2	2.0	0%	0%
2012	1	2	2.0	0%	50%
2013	1	2	2.0	50%	—
2014	1	3	3.0	33%	0%
2015	0	0	—	—	—
2016	0[b]	0	—	—	—
2017	0	0	—	—	—
2018	0	0	—	—	—
2019	0	0	—	—	—
2020	1	3	3.0	33%	—
Overall	30	68	2.3	47%	25%

[a] Blanks indicate no cub mortality data because no cubs were born to collared females, or collared mothers were lost from study (died or lost collar) before denning with yearlings.
[b] One bear that likely had cubs was not checked because access to her den was precluded by poor ice conditions.

Table 7. Intervals between litters (where at least 1 cub survived) for black bears within 4 study sites in Minnesota through March 2020 (CNF since 1981, Camp Ripley since 1991, VNP since 1997, NW since 2007). Cubs typically remain with their mother for about 17 months, so the normal reproductive interval is 2 years.

Study area	2-year reproductive intervals	≥3-year reproductive intervals	% intervals ≥3 years
CNF	115	8	7%
Camp Ripley	37	5	12%
VNP	15	1	6%
NW	20	0[a]	0%

[a] Excluding 1 missed litter (3-year interval) that was due to the bear leaving the den after disturbance and aborting the litter.

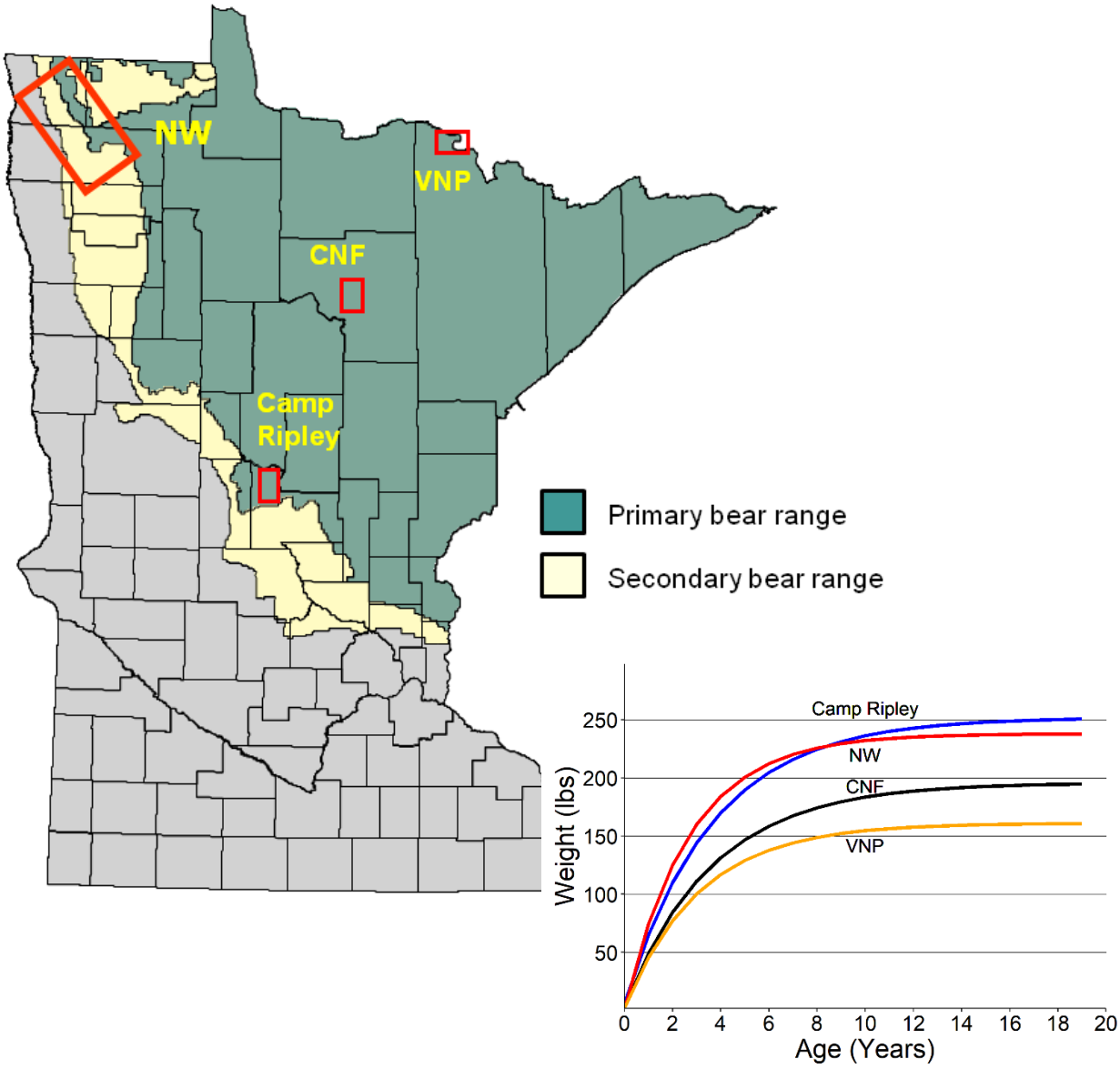

Figure 1. Location of 4 study sites within Minnesota's bear range: CNF (Chippewa National Forest, central bear range; 1981–2020); VNP (Voyageurs National Park, northern fringe of range; 1997–2020); Camp Ripley Military Reserve (near southern edge of range; 1991–2020); NW (northwestern fringe of range; 2007–2020). Inset shows non-linear regressions of weights of female bears of each age during February–March (late denning).

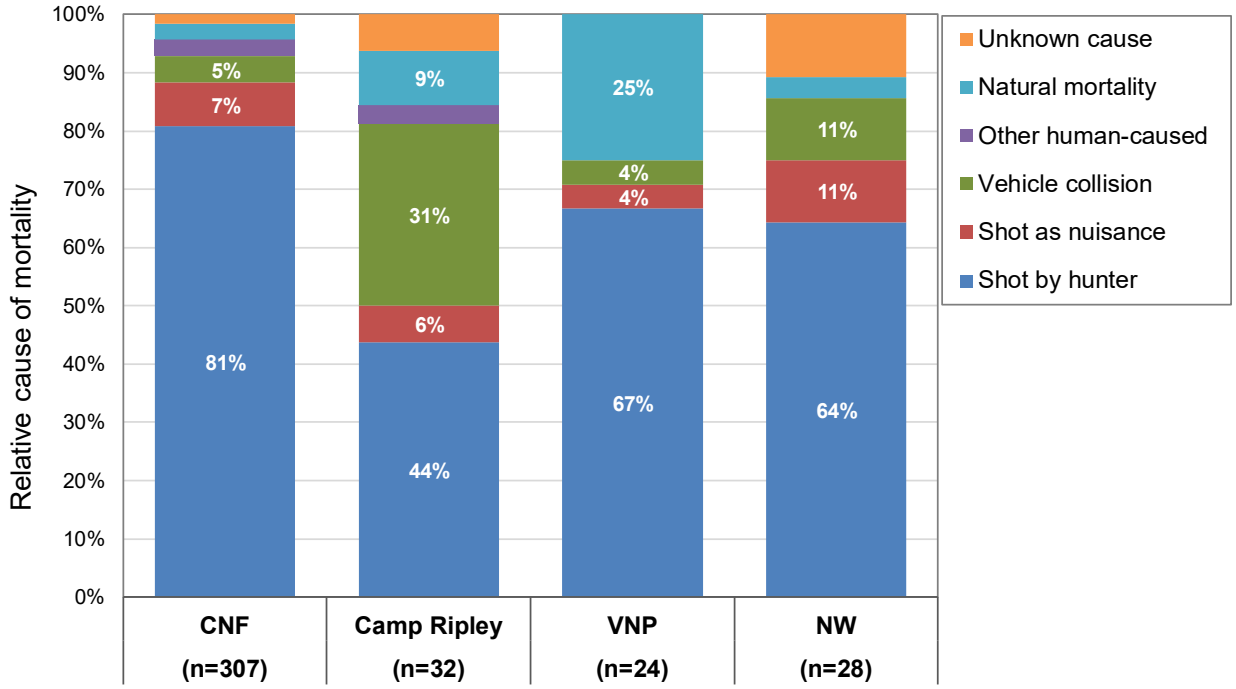

Figure 2. Proportional causes of death of radiocollared bears in each of 4 study sites in Minnesota, since the beginning of the study in each area through the winter of 2019–2020 (see map and dates for each study site in Figure 1). CNF expectedly had the highest proportion of bears killed by hunters because this is primarily public land that is heavily hunted. Camp Ripley and VNP are unhunted but bears are vulnerable when they leave on foraging forays. Hunters were asked not to shoot collared bears during the entire span of the NW study, so the proportion of mortality due to hunting for non-collared bears in that area would likely be considerably higher than shown here.

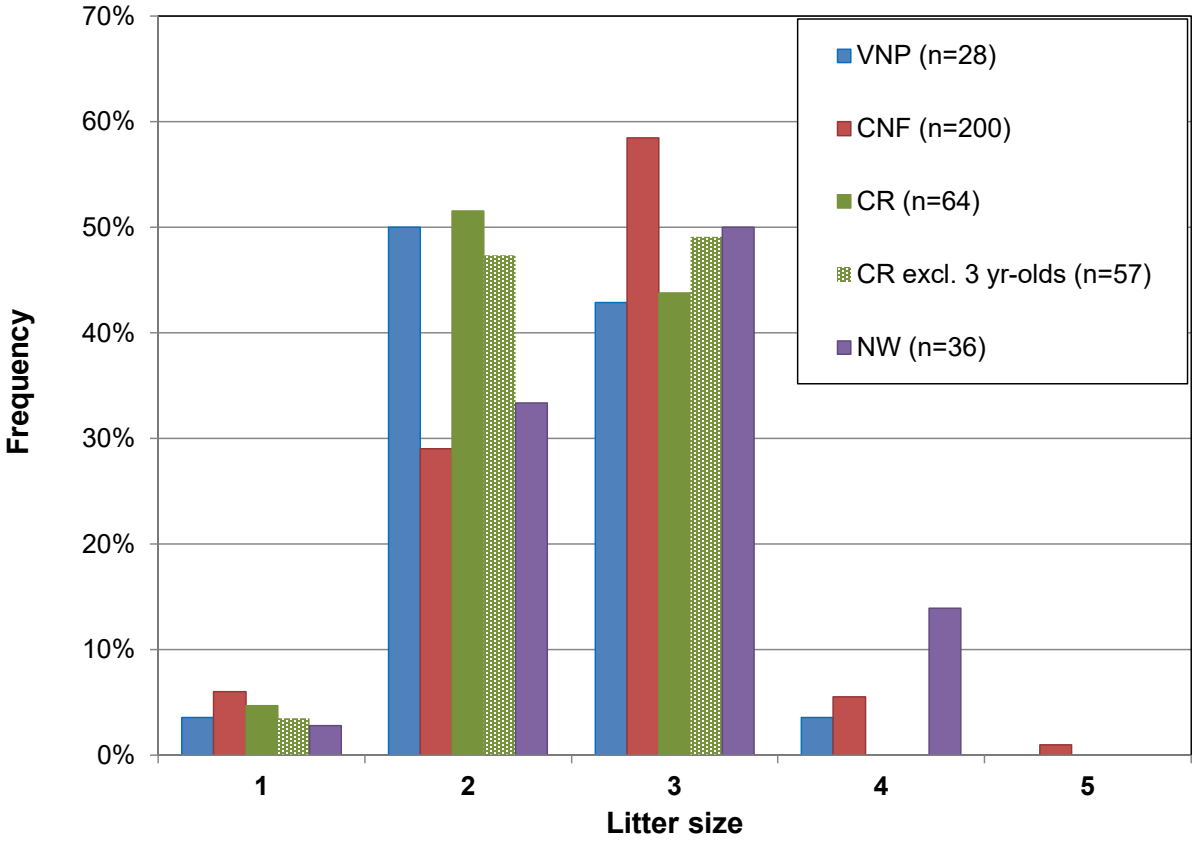

Figure 3. Frequency of cub litter sizes (examined in natal dens in March) within 4 Minnesota study sites (see Figure 1) through March 2020. Data include only litters in which at least 1 cub survived 1 year. Camp Ripley data are shown for mothers of all ages, as well as excluding 3-year-old mothers, which had smaller litters. For the other sites, elimination of 3-year-olds did not make a difference.

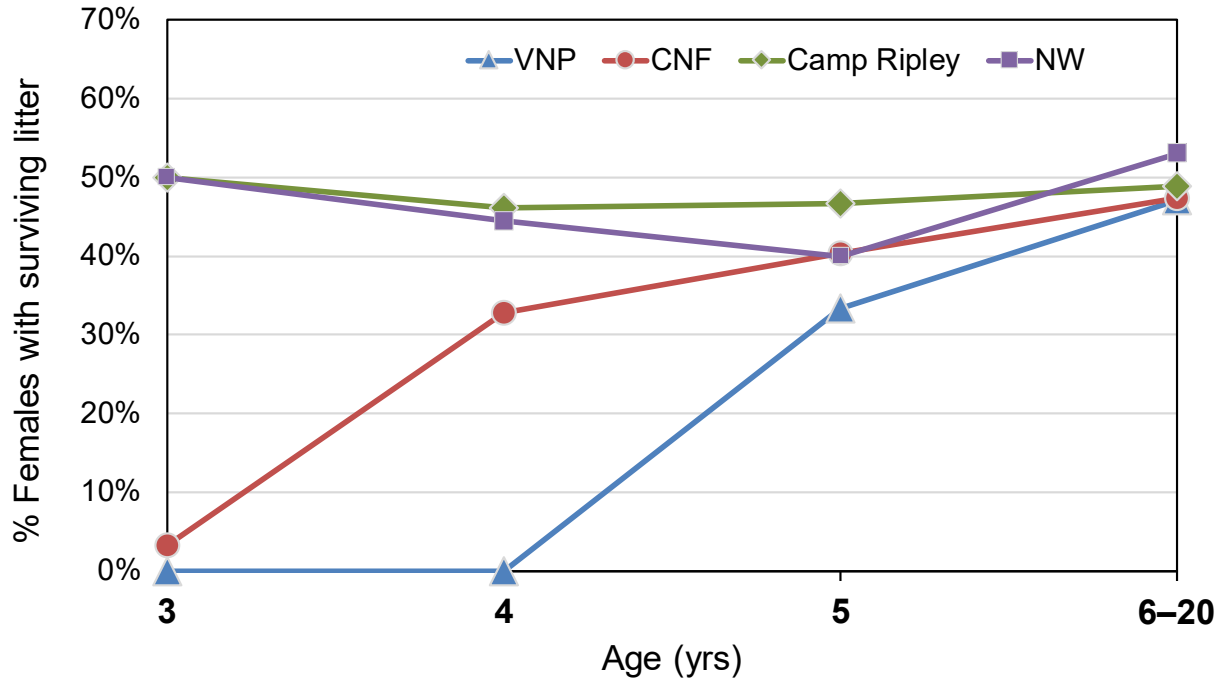

Figure 4. Percent of females producing a litter in which at least 1 cub survived until becoming a yearling (observed in the den) in each of the 4 Minnesota study sites through March 2020. Females matured earliest (half of them at 3 years old) in Camp Ripley and NW, and were most delayed in VNP (none produced cubs before age 5). Once producing cubs, most bears gave birth at 2-year intervals (Table 7), so by age 6, about half produced each year.

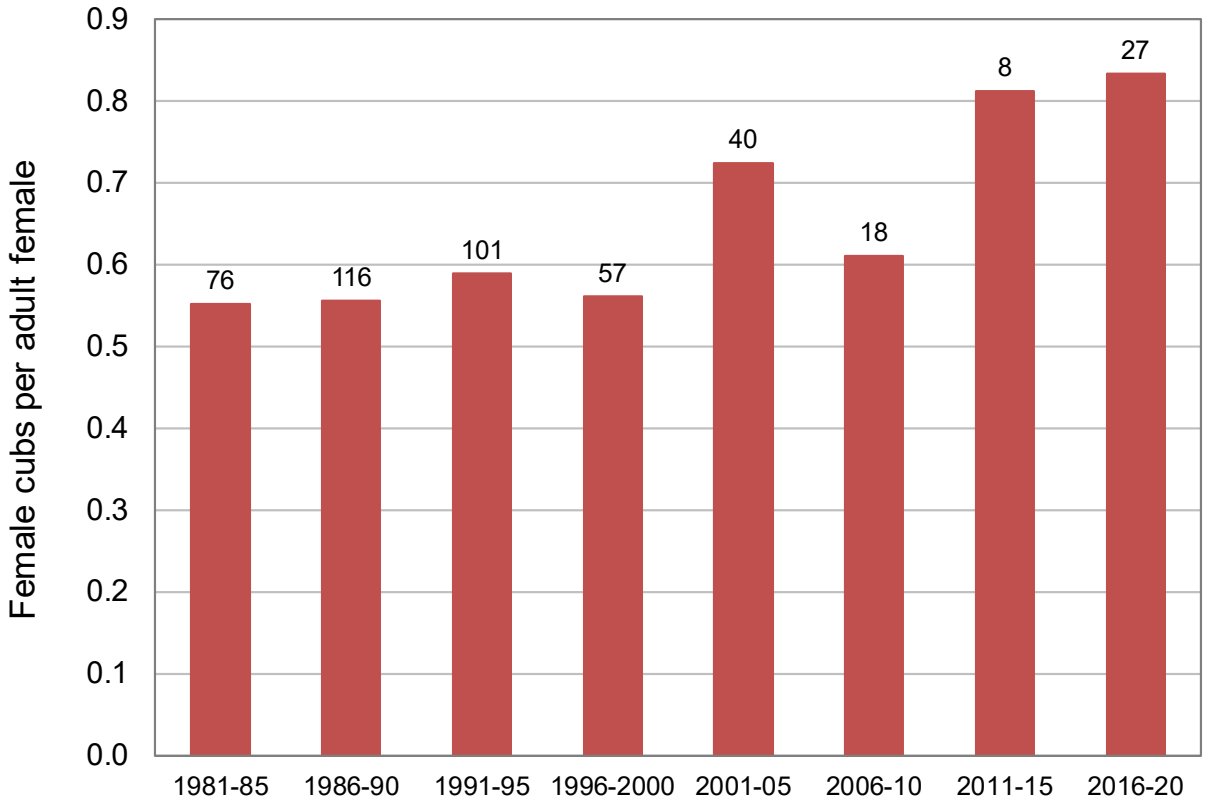

Figure 5. Reproductive rate of 4+ year-old female bears in CNF, Minnesota, study site, measured as female cubs produced (total cubs/2) divided by bear-years of monitoring (indicated by number above bar; 1 bear-year = 1 female bear observed at a den) for 5-year increments since study began. Data exclude litters in which no cubs survived. If all females produced 2.7 cubs (the long-term average at this site) every 2 years, the reproductive rate would be (2.7/2)/2 = 0.675. However, because less than half the females in the CNF produced cubs at 4 or 5 years old (Figure 4), the reproductive rate was generally <0.6. The seeming increase since 2011 may, in part, be a vagary of small sample size (see text).