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Seasonal migrations of black bears (*Ursus americanus*): causes and consequences

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Abstract American black bears frequently abandon their home ranges in late summer and move to feeding areas to fatten themselves for hibernation. We examined seasonal movements of 206 radio-collared bears in north-central Minnesota during 1981–1990. We exploited the variability in this long-term data set to test tradeoffs for animals leaving their home range. Late summer movements were common for both sexes and all ages (39% of females, 44% of males), but were variable from year-to-year in prevalence, timing, and destination. Bears typically left their summer home ranges in August and returned ~6 weeks later in September or October. Most traveled southward, where acorns were more plentiful (median = 10 km for females, 26 km for males; maximum = 168 km). These facultative migrations were most common when rich resources were available outside home ranges. Bears were least apt to leave when foods were scarce in their home range, possibly sensing a risk of migrating during a widespread food failure. Among females, those whose body mass was close to a reproductive threshold were most prone to migrate. Migrating bears were less likely to be killed by hunters, suggesting that they were especially vigilant.

Keywords Cost/benefit trade-offs · Food abundance · Hunting mortality · Oak mast · Reproductive threshold · Seasonal movements

Introduction

Animals that rely on geographically shifting resources can either move with those resources or stay put and withstand periods of scarcity. Consistent seasonal changes in resource distribution give rise to the predictable migratory patterns found in a broad range of species (Dingle 1996). More variable conditions favor behavioral flexibility that enables animals to adjust movements from year to year in accordance with resource availability (Newton 2006).

Animals that travel outside their familiar territory in an attempt to find better food sources are subject to heightened risk. Travel itself is energetically costly (Alerstam et al. 2003) and extra time and energy may be required to locate food and navigate in novel surroundings. Lack of familiarity with local conditions may increase exposure to harm (Nicholson et al. 1997) and the need for extra vigilance can reduce foraging efficiency (Brown et al. 1999). In travelling to unfamiliar places, animals ultimately risk failing to find better foods than those they left behind (John and Roskell 1985). To be adaptive, travel must provide sufficient benefit to offset these costs and enhance reproduction or survival (Brönmark et al. 2008).

American black bears are generally not recognized as typical “round-trip” migrators (Dingle 1996), yet there are many accounts of their long-distance movements to concentrated food sources in late summer and fall (up to 200 km; Rogers 1987a). These travels occur during a time of hyperphagia, when bears extend daily foraging time (Garshelis and Pelton 1980; Lariviere et al. 1994) and increase caloric consumption (Hashimoto and Yasutake 1999; Hilderbrand et al. 1999) in preparation for hibernation. The specific foods they seek vary geographically, but most are fruits or nuts that exhibit pronounced stochasticity in annual yield (Koenig and Knops 2000; McShea

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and Schwede 1993; Noyce and Coy 1990). Variability in the prevalence and geographic extent of seasonal travel, both within and among bear populations, has confounded the development of a cohesive explanation of this behavior.

The sporadic late-summer movements of bears resemble the “partial,” “facultative,” and sometimes “irruptive” migrations described for other vertebrate species (Newton 2006; Olsson et al. 2006; White et al. 2007). As in other facultative migrators (Newton 2006), food scarcity is generally thought to trigger such movements (Hellgren et al. 2005; Schorger 1946). However, contradictory observations have also been reported (Kasbohm et al. 1998; Rogers 1987a; Schooley et al. 1994).

As for a host of migratory species (Dingle 1996), the potential for gain or loss in undertaking seasonal travel will differ among individuals by sex, age, size, reproductive status, and local habitat conditions. Bears also are constrained in that, instead of moving to better food conditions and remaining there during the period of food scarcity, their movements are directed at finding sufficient food to store as fat to survive an extended winter fast (hibernation). Females that find rich food supplies in the fall may aid the growth and survival of cubs traveling with them or yet unborn (Noyce and Garshelis 1994). Males that increase growth in the fall may enhance the likelihood of siring cubs the following spring (Kovach and Powell 2003; Costello et al. 2009). However, animals that move into unfamiliar areas may suffer greater mortality (Hellgren et al. 2005; Pelton 1989; Schwartz and Franzmann 1992), so this must be weighed against the potential benefits.

Here, we document the late-summer movements of Minnesota black bears over a 10-year period and exploit the variability we observed to test the following hypotheses: (1) Individuals leave their summer ranges if the likelihood is high that they will find better food elsewhere, (2) individuals are most likely to travel in search of better foods if their body mass is close to a reproductive or survival threshold, and (3) travel behavior reflects decisions that minimize risk. We investigate the influence of sex, age, body size, natural food abundance, and habitat, and interpret results from a risk–benefit perspective.

Materials and methods

Study site

The study area encompassed 360 km² in the Chippewa National Forest (CNF) and adjoining George Washington State Forest (47°30'N, 93°30'W) in north-central Minnesota. The terrain was >95% forested and shaped by Pleistocene glaciations. A distinct ecotone divided the hilly St. Louis

Moraines (SM) landscape of mixed uplands, lowlands, and lakes, from the flat lowland landscape of the Chippewa Plains (CP) glacial outwash (Minnesota Department of Natural Resources 2003). Female bears living near this ecotone exhibited a strong fidelity to either SM or CP during most of the year, whereas males traversed larger, more heterogeneous areas. Upland forests, comprising about 67% of the study area, were an aspen-dominated mix (*Populus tremuloides*, *Betula papyrifera*, and *Abies balsamea*), with scattered pine (*Pinus resinosa* and *Pinus strobus*) and hardwoods (*Acer saccharum*, *Tilia americana*, and *Quercus rubra*). Lowland forests contained mainly black spruce (*Picea mariana*), tamarack (*Larix laricina*), northern white cedar (*Thuja occidentalis*), and black ash (*Fraxinus nigra*).

Principal fruits available to bears during July–August included wild sarsaparilla (*Aralia nudicaulis*), blueberries (*Vaccinium* spp.), raspberries (*Rubus idaeus*), Juneberries (*Amelanchier* spp.), and cherries (*Prunus virginiana* and *Prunus pennsylvanica*). Dogwood berries (*Cornus* spp.), hazelnuts (*Corylus cornuta*), and acorns, primarily of red oak (*Q. rubra*), were the main foods during late August–September. Berry and nut production was highly variable from year to year (Noyce and Coy 1990), which was reflected in bears' diets (Garshelis and Noyce 2008). Lowland habitats produced less berry and nut biomass than upland habitats (Noyce and Coy 1990).

The study area supported timber production, seasonal homes, and forest- and lake-centered recreation. Two open landfills were used regularly by bears until 1986, when they were converted to secure dumpsters. Bear hunting was legal from September 1 to mid-October, and most hunters attracted bears with bait. Bear density was ca. 20 bears/100 km² (Garshelis and Noyce 2008) and harvest density was among the highest in the state (on average, >6 bears killed/100 km²).

Delineation of home range and seasonal movements

Bears were captured in baited barrel traps or Aldrich foot snares and fitted with VHF radio-collars (Telonics, Mesa, AZ, USA) during May–July, 1981–1989. Radio-collared bears were handled annually in their winter dens, at which time yearlings (denned with their mothers) were fitted with radio-collars. We immobilized bears with ketamine hydrochloride (11–13 mg/kg) and xylazine (0.6–0.7 mg/kg), or premixed tiletamine hydrochloride and zolazepam (Telazol®, Elkins-Sinn, Cherry Hill, NJ, USA, 3.9–5.3 mg/kg). At first handling, we extracted a first upper premolar for estimating age and discerning reproductive history (Coy and Garshelis 1992; Willey 1974). Bears were weighed with hanging spring scales and body measurements were recorded to the nearest centimeter. Handling procedures were in accordance with companion work that was approved by the Institutional

Animal Care and Use Committee of the University of Minnesota. Radio-collared bears were located from fixed-wing aircraft during daylight hours at intervals of 3–5 days in 1981–1982, 6–9 days in 1983–1984, and weekly or bi-weekly during 1985–1990.

We defined a bear's summer home range (or simply home range or home) as the area where it centered its activities for most of the year, including, as a minimum, the mid-May to mid-July breeding season. Departures from the home range were easily identified by a sudden, distinct traverse to a new area. We delimited the summer home range using a minimum convex polygon (MCP) encompassing all telemetry locations within 2 km (females) or 5 km (males) of at least one other point in the cluster. Beyond those distances, locations were considered movements outside the summer range (Fig. 1a). Using these criteria, nearly all points were included within the home range during early summer, when bears traveled little, but these thresholds were exceeded at other times of the year, enabling us to detect movements to new areas. To delineate MCPs, we pooled locations across years for individual bears, unless home range shifts between years were evident. We measured movements outside the home range along a perpendicular line from the perimeter of the MCP to the most distant location (Fig. 1b). Direction of travel was measured to the same point from the geographic center of the MCP.

We classified movements as either seasonal forays (moves from which bears returned) or dispersal (permanent departures of bears known to be born in the study area). We separated seasonal forays by the time of year that they occurred: (1) early season, commencing April–June, with return usually before mid-July; (2) late season, initiated after 1 July, with return typically after 1 September; or (3) overwinter, to dens outside the summer

home range, with return in the spring. We focus this paper primarily on the characteristics and causes of late-season forays.

We could not precisely define the timing and duration of seasonal forays because individuals often left their home range abruptly and traveled quickly, so we often could not find them for a week or more after they left. Thus, instead of estimating departure dates, we used the date of each bear's last known location within its summer range. This way, bears that traveled farther did not appear to leave later simply as an artifact of the difficulty in finding them. Similarly, for their returns, we used the date that we detected them back in their summer range. Since we routinely monitored all radio-collar frequencies in the central study area, we were apt to note the disappearance of bears shortly after their leaving and likewise hear their radio signals shortly after they arrived back from forays.

Assessment of foods

We investigated the relationship between the abundance of natural foods (fruits and nuts) and year-to-year differences in the late summer movements of bears. Natural resources personnel across the bear range in Minnesota provided annual ratings of fruit production, on a 0–4 scale (2 = “average”), for each of 14 different food types (Noyce and Garshelis 1997). We used surveys conducted within ≈40 km of the study area in conjunction with our ratings in the study area to characterize local food abundance. To corroborate indices, we quantified fruits and hazelnuts in 45–100 forest stands during 1984–1989 (Noyce and Coy 1990). Acorns were counted separately, sampling ten trees each year (1982–1990) in six red oak and 1–2 bur oak (*Quercus macrocarpa*) stands (Whitehead 1969).

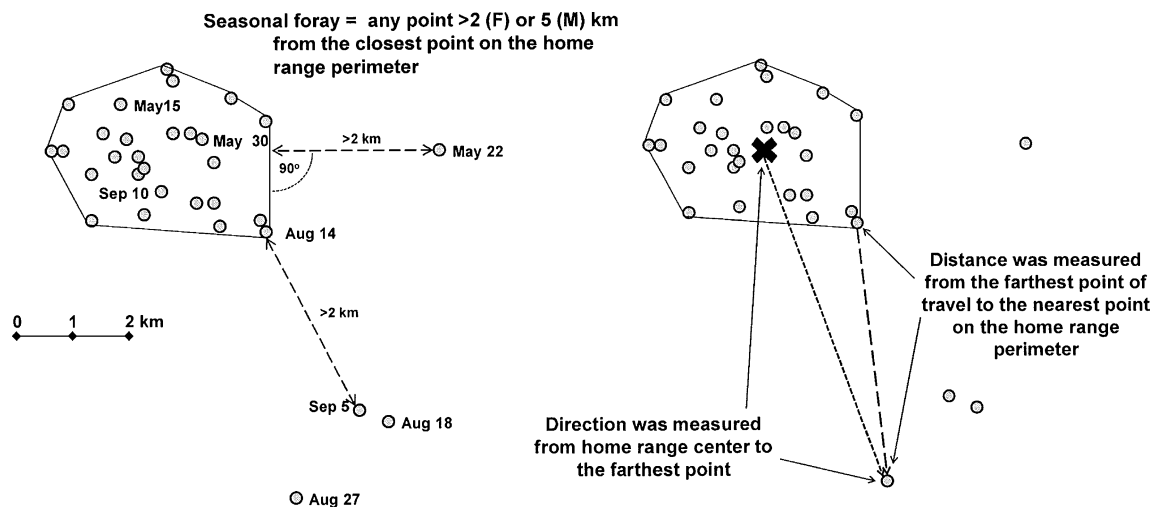


Fig. 1 Delineation of MCP home ranges and method for defining and measuring movements by black bears outside their summer range

Data analysis

We used chi-square analysis to test for differences in the frequency of seasonal movements outside the summer home range by sex, age (1, 2, 3, and >4 years old [adult]), and reproductive class. We compared mean duration and median distance of early vs late-season travel using two-sample *t* tests and Kruskal–Wallace nonparametric AOV. We grouped bears by azimuth of travel (12 groups, each spanning 30° of arc) and used chi-square to compare travel orientation of males and females and chi-square goodness-of-fit to test for deviation from random.

We modeled the effects of sex, age, and abundance of key bear foods on the likelihood, timing, distance, and duration of late season movement using logistic and linear regression, and compared models with Akaike's information criterion (AIC_c). For food covariates, we used the annual local (within ≈40 km) productivity indices of oak, hazel, chokecherry, and sarsaparilla, raspberry, and chokecherry, summed (three important summer foods). To allow for non-ordinal effects, we represented age as two binary (0,1) parameters that separately identified 2-year-olds and 3+-year-olds, with yearlings as the reference group. Collinearity of parameters was acceptable (variance inflation factors for main covariates ≤3.0). We posed two a priori models, one including covariates for food abundance (with interactions) and one without. We sequentially eliminated the least important covariate, identified by minimal absolute value of *b*/SE (Arnold 2010), continuing until elimination of additional covariates increased AIC_c by ≥2.0. When a covariate was identified as unimportant, we first eliminated interaction terms involving that covariate, only then eliminating the main covariate, if still warranted. If two covariates had equivalent scores, we modeled each elimination separately, then continued eliminations from both of these models. Tables present a priori models, plus the three or four best reduced models so derived, recognizing that there is debate regarding the best method for defining a set of candidate models (Arnold 2010; Symonds and Moussalli 2010). For females, we modeled the effect of body mass and home range landscape (CP or SM) on the likelihood of late-season travel. We categorized body mass as: <25 kg, 25–34.9 kg, 35–49.9 kg, 50–69.9 kg, and ≥70 kg. In one model, to allow for non-ordinal effects, the higher categories were represented as four separate binomial parameters, with bears weighing <25 kg comprising the reference group. Each year that an individual bear was monitored constituted one record. Though we recognize that multiple records for individuals may not be fully independent, the degree of behavioral variation that we observed within individuals from year to year indicated that the effect of the individual was minor relative to other covariates.

We compared daily survival of bears that remained within their home range vs those that traveled outside during the first 2 weeks of fall bear hunting, using the Gehan–Wilcoxon two-sample survival test (Statistix 9, 2008, Analytical Software, Tallahassee, FL, USA). Hunter kills and locations were ascertained through mandatory hunter reporting.

Results

During 1981–1990, we tracked the movements of 206 individual bears (82 females, 124 males), aged 1–19 years old. Individuals were monitored 1–10 years each, totaling 540 bear-years (297 female, 243 male); 62 females and 65 males were followed multiple years. Travel outside the summer home range was common for both sexes, occurring in 43% (F) and 70% (M) of bear-years monitored (Table 1). Two-year-olds of both sexes were the most likely to travel (females: $\chi^2=13.5$, *df*=4, *P*=0.004; males: $\chi^2=13.9$, *df*=3, *P*=0.003). All males born in the study area either dispersed (*n*=27), died, or were otherwise lost from the study by age 4, whereas only one of 42 females dispersed. Dispersal occurred during all non-hibernating months (April–November) with nomadic movements spanning 5 days to months, sometimes >1 year.

Early-season forays (April–June) were made by 8% of bears, but were most common for 3-year-old females and 2-year-old males (Table 1; females: $\chi^2=15.3$, *df*=4, *P*=0.004; males: $\chi^2=14.4$, *df*=3, *P*=0.002). Median movement was 3 km for females and 9 km for males, about half the typical length of the long axis of the average home range; maximum distances were 41 km and 83 km, respectively. Early-season forays showed no predominant orientation ($\chi^2=4.3$, *df*=11, *P*=0.96). Males typically stayed away longer than females (mean: 27 vs 17 days, respectively). Of eight subadult (preparous) females that made early-season forays, seven were of breeding age and size; three were later confirmed to have been in estrus that spring. Of five adult females making early-season forays, four (three with cubs, one with yearlings) traveled to active garbage dumps.

Late-season forays were more common than early-season forays (Table 1). Of bears that we tracked for ≥3 consecutive years, 87% made at least one late-season foray (41 of 47 females, 24 of 28 males; median years tracked: 4.5 for females, 4.0 for males). However, only 10 of 35 females and two of 15 males tracked ≥4 years made late season forays in 3 consecutive years. The proportion of bears that moved varied from year to year (range: 25–64% of juveniles, 3–87% of adults). For females, this appeared unrelated to whether they had cubs (Table 1). Late-season forays were longer in distance (median = 10 km for females

Table 1 Percent of radio-collared bears of each sex and age that moved outside their regular summer home range in a year, north-central Minnesota, USA, 1981–1990

Sex-age of bear	Number	Early season (April–Jun) %	Late season (Jul–Sep) %	Overwinter %	Dispersal %	All types %
Females:						
1 year old	46	2	29	4	0	31 ^a
2 years old	36	0	64	8	3	69
3 years old	39	15	31	8	3	41
Adult with cubs	78 ^b	5	42	4	0	49
Adult no cubs	98 ^b	2	34	1	0	36
All	297 ^b	4	39	4		43
Males:						
1 year old	60	10	42	5	17 ^c	61
2 years old	53	23	33	17	48 ^c	90
3 years old	39	13	56	23	5 ^c	69
Adult	91 ^b	8	47	27	1 ^{cd}	65
All	243 ^b	12	44	20		70

^a Some bears made more than one type of movement in a year; thus, columns do not sum to this value

^b Bears monitored for >1 year provide a data record for each full year monitored, thus some individuals account for >1 record in the adult age class

^c Although all males born on the study area dispersed, percentages of males shown here dispersing at each age do not sum to 100% because many bears included had already dispersed from elsewhere into the study area

^d The oldest male to disperse left his natal range at 4 years old

[$\chi^2=10.3$, $df=1$, $P=0.0013$], 26 km for males [$\chi^2=16.08$, $df=1$, $P=0.0001$] and in duration (mean = 39 days for females [$t=3.9$, $df=131$, $P=0.0002$]), 46 days for males [$t=3.8$, $df=111$, $P=0.0002$]) than early-season travels. Movement was strongly directional (females: $\chi^2=67.0$, $df=11$, $P<0.0001$; males: $\chi^2=88.8$, $df=11$, $P=0.0001$), tending to the south and southwest (Fig. 2). Direction of movement differed for males and females, suggesting segregation in fall feeding areas ($\chi^2=29.4$, $df=11$, $P=0.002$). Though departure from home ranges occurred from early July to late October, most bears left during late July and August, with 35% departing between July 29 and August 11. Most returned home in September or early October, but 25% of males on forays moved up to 144 km (median = 49 km, $n=47$) directly from late-season foraging areas to den sites outside their summer home range (usually to the north) and did not return home until spring (Table 1). Late-season and overwinter travels easily fit the definition of migration in being: (1) highly seasonal, directional, and outside the home range; (2) conducted by many individuals; (3) resulting in a redistribution of the population; and (4) temporary, from which individuals eventually returned home (Dingle 1996, Dingle and Drake 2007).

Regression modeling indicated that food availability influenced migration behavior; in all cases, addition of food covariates markedly improved model fits (Tables 2A and 3, all models II vs III; Table 2B, models II and III vs IV). The best-supported reduced models (Ia–d) all included ≥ 3 food covariates, along with various sex \times food and

age \times food interactions. Oak (acorn) abundance had the largest effect on probability of travel: for example, when we set sex and age at “0” (=yearling male) and held other food indices constant, model Ia (Table 2, A) predicted that an increase from 1 to 2 in the acorn index added 0.14 to the calculated probability of migration. The same increase in hazel or summer food index (holding others constant) added only 0.01–0.02. The influence of acorn abundance was greatest for adults (age \times oak, model Id, Table 2, A); with other foods constant, an increase from 1 to 3 in the oak index (representing a change from “below average” to

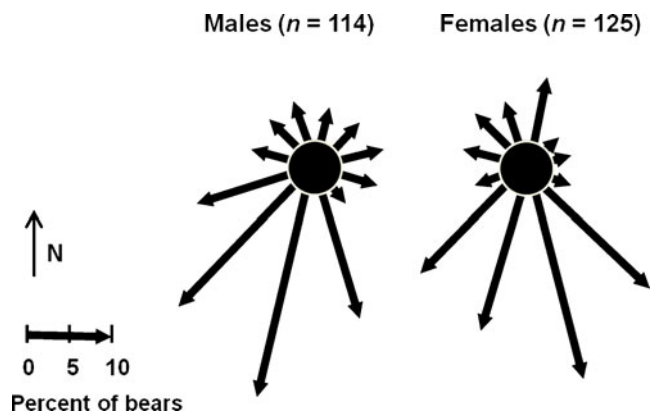


Fig. 2 Direction of late-season forays made by male and female black bears in north-central Minnesota. Arrows represent 30° increments in travel orientation and the length of each arrow represents the percent of forays oriented in that direction. Travel orientation differed between males and females and differed from random for both sexes

Table 2 Akaike's information criterion (AIC_c) model selection for logistic regressions of probability of late-summer migration by black bears in north-central Minnesota as a function of sex, age, natural food availability, home range habitat, and body mass

Sample	Model ^a	Model covariates ^b	Deviance	K	AIC _c	ΔAIC _c
A. All bears (n=542)	Ia	SX + A(2) + O + S + H + SX×A(2) + SX×H + SX×S	657.2	11	679.7	0.0
	Ib	SX + A(2) + O + S + Ch + H + SX×A(2) + SX×H	657.2	11	679.7	0.0
	Ic	SX + A(2) + O + S + Ch + SX×A(2) + SX×O	659.73	10	680.1	+0.4
	Id	SX + A(2) + O + S + Ch + H + SX×A(2) + SX×Ch + SX×S + SX×H + A(2)×O + A(2)×Ch	645.9	17	681.1	+1.4
	II	SX + A(2) + O + S + Ch + H + SX×A(2) + SX×O + SX×Ch + SX×S + SX×H + A(2)×O + A(2)×H + A(2)×C + A(2)×S	642.5	22	688.4	+8.7
III	SX + A(2) + SX×A(2)	720.5	6	726.7	+47.0	
B. Females ^c (n=185)	Ia	A(2) + L + WT + O + S + Ch + H + A(2)×Ch	195.2	11	218.7	0.0
	Ib	A(2) + L + O + S + Ch + H + A(2)×Ch	198.6	10	219.6	+0.9
	Ic	A(2) + L + WT + O + S + Ch + H	200.9	9	219.9	+1.2
	Id	A(2) + L + WT + O + S + Ch + H + A(2)×Ch + A(2)×WT	192.7	13	220.8	+2.1
	II	A(2) + L + WT + A(2)×WT + O + S + Ch + H + A(2)×O + A(2)×S + A(2)×Ch + A(2)×H	191.5	19	231.0	+12.3
	III	A(2) + L + O + S + Ch + H + A(2)×O + A(2)×S + A(2)×Ch + A(2)×H	197.2	16	232.4	+13.7
	IV	A(2) + L	237.6	4	245.8	+28.4

^a Models Ia–d represent the best-fitting models, based on AIC_c derived by reduction from a priori models II–IV. A priori models are included to highlight the importance of food abundance in explaining likelihood of migration

^b Model covariates: SX sex, A(2) age represented as two binomial parameters, L Landscape (SM uplands or CP lowlands), O oak production index, S summed fruit production indices of wild sarsaparilla, raspberry, and chokecherry (important mid-summer bear foods, chosen based on prevalence in scats), Ch chokecherry production index, H hazel production index

^c Model B includes covariates for landscape type (only females showed landscape fidelity in their summer home ranges) and body mass, standardized by date

“above average”) added a substantial 0.39 to the estimated migration probability for adults, but only 0.13 for yearlings. In 1988, when acorns were the most plentiful, 26 of 29 adults migrated vs only one of 28 in 1985, when acorns (and most other bear foods) failed (Fig. 3a). However, bears that migrated during poor acorn years often traveled far. A single adult male that migrated in 1985, and three of six that did so in 1990 (another poor year), made four of the five longest moves recorded during this study (114–168 km, one-way, straight-line).

Model Id (Table 2, A) suggested that chokecherry abundance was particularly significant for young females; a change from 1 to 3 in the index added 0.11–0.16 to migration probability for females <3 years old, but had negligible effect on other bears (sex × chokecherry and age × chokecherry). The same change in hazel added 0.17 to the migration probability for females, but not males (Table 2, A, model Id, sex × hazel). All models (Table 2, A), indicated that 2-year-old females and adult males were most likely to migrate and yearling females least likely (sex × age). Two-year-old males exhibited less migration than other males because many were dispersing.

Among females (Table 2, B, Ia–d), the odds of migrating were 2.1–2.4 times higher for those living in lowland landscapes than for those in uplands. Model Id suggested an age × weight interaction wherein heavy yearlings (25–

34.9 kg) were more likely to migrate than lightweight yearlings (<25 kg), but in older bears (all ≥35 kg), lightweight individuals (35–49.9 kg) were more likely to move.

Differences in the timing, distance, and duration of late-season travels were also influenced by sex, age, and food abundance (Table 3). Males 1–2 years old generally left home earlier, traveled farther, and stayed away longer than older bears (Tables 3 and 4, all models, sex and age effects); 1 and 2-year-old females were away the shortest time. High hazelnut abundance prompted females to move sooner than usual, but not males (Table 3, A, models Ia–Id, sex × hazel interaction). Bears left sooner, traveled farther, and stayed away longer when acorns were plentiful (Table 3, all models I and II, oak effect) and they tended to leave later when chokecherry was abundant (Table 3, A, models Ia–Ic, chokecherry effect). In 1988, a year with outstanding acorn production and good summer berry production (albeit cut short by a July drought), bears left home ranges particularly early (Table 4). Conversely, in 1983, when berry production (especially chokecherry) was the best in this study, most bears delayed their migrations by 3–6 weeks compared to 1988. We discerned no effect of covariates on migration return dates.

Females living near the interface of the CP lowlands and the SM uplands provided an enlightening example of

Table 3 Akaike's information criterion (AIC_c) selection for linear regression models of departure dates, duration, and distance of seasonal black bear migrations, as a function of sex, age, and natural food availability in north-central Minnesota

Response	Model ^a	Model covariates ^b	K	AIC _c	ΔAIC _c	Adj R ²
A. Departure date	Ia	SX + A(2) + O + Ch + H + SX×H + A(2)×H + A(2)×Ch	12	1,339.2	0.0	0.18
	Ib	SX + A(2) + O + S + Ch + H + SX×S + SX×H + A(2)×H + A(2)×Ch	14	1,340.3	+1.1	0.19
	Ic	SX + A(2) + O + S + Ch + H + SX×O + SX×S + SX×H + A(2)×H + A(2)×Ch	15	1,341.9	+2.7	0.18
	II	SX + A(2) + O + S + Ch + H + SX×A(2) + SX×O + SX×Ch + SX×S + SX×H + A(2)×O + A(2)×H + A(2)×Ch + A(2)×S	22	1,353.4	+13.2	0.18
	III	SX + A(2) + SX×A(2)	6	1,372	+32.8	0.02
B. Duration	Ia	SX + O + Ch + H + SX×O + SX×Ch + SX×H	8	1,094.8	0.0	0.16
	Ib	SX + A(2) + O + Ch + H + SX×O + SX×Ch + SX×H + A(2)×Ch	12	1,098.3	+3.5	0.17
	Ic	SX + A(2) + O + Ch + H + SX×O + SX×Ch + SX×H + A(2)×O, A(2)×Ch	14	1,098.7	+3.9	0.18
	II	SX + A(2) + O + S + Ch + H + SX×A(2) + SX×O + SX×Ch + SX×S + SX×H + A(2)×O + A(2)×H + A(2)×Ch + A(2)×S	22	1,115.6	+21.8	0.16
	III	SX + A(2) + SX×A(2)	6	1,123	+28.2	0.01
C. Log (distance) ^c	Ia	SX + A(2) + O + H + S + SX×O + SX×S + SX×H	10	-436.9	0.0	0.38
	Ib	SX + O + S + H + SX×O + SX×S + SX×H	8	-435.1	+1.8	0.37
	Ic	SX + A(2) + O + Ch + H + S + SX×O + SX×S + SX×H	11	-435.0	+1.9	0.38
	II	SX + A(2) + O + S + Ch + H + SX×A(2) + SX×O + SX×Ch + SX×S + SX×H + A(2)×O + A(2)×H + A(2)×Ch + A(2)×S	22	-416.4	+20.4	0.36
	III	SX + A(2) + SX×A(2)	6	-395.2	+39.8	0.23

^a Models Ia–c represent the best-fitting models, based on AIC_c derived by reduction from a priori models II and III. A priori models are included to highlight the importance of food abundance in explaining migration characteristics

^b Model covariates: SX sex, A(2) age represented as two binomial parameters, O oak production index, S summed production indices of wild sarsaparilla, raspberry, and chokecherry, important mid-summer bear foods, chosen based on prevalence in scats, Ch chokecherry production index, H hazel production index

^c Distance values were highly skewed, so were log-transformed to achieve normal distribution

within-population variation in migration behavior. Both upland and lowland females exhibited strong fidelity to their home landscape during spring and early summer. However, in late summer, lowland females commonly (30 of 60 bear years sampled) left their home range and most often (87% of the time, excluding 1988) traveled to the Suomi Hills, with the highest density of red oaks in the study area. Only one male was located in Suomi Hills during that time of year. Males tended to travel farther south, to areas only occasionally visited by radio-collared females. Females that lived in the Suomi Hills, however, rarely left home (Fig. 4a, b).

In 1988, when acorn production (particularly bur oak) was exceptionally high (index 3.3 vs mean 1.9), almost all collared adult females, including all but one from Suomi Hills, left their summer range (Fig. 4c, d) and traveled up to 60 km (mean 20 km) to late-summer feeding areas. That year, females bypassed the Suomi Hills and continued farther south and southwest to novel destinations where bur oak (*Q. macrocarpa*), which was rare in the study area, was more common. Though we were generally unable to detect differences in body mass, growth, or reproduction that could be attributed to migration, eight lactating females that migrated with their cubs in 1988 lost less weight between winters (\bar{x} = 8.5kg, range 4–16 kg; \bar{x} = 11.5% of body

mass lost, range 5–22%) than the sole lactating female that did not migrate (20 kg=24% of body mass).

Contrary to expectation, migrating bears were no more vulnerable to hunters than non-migrators. In fact, during the first week of the hunting season (1–7 Sept), when most bears were killed, hunting mortality was higher for females that remained at home than for those that migrated (Cox's F test: $F_{(52,2)}=0.23$, $P=0.03$). This was also true for males, but not significantly so ($F_{(46,20)}=0.61$, $P=0.17$; Fig. 5). Hunting mortality during later weeks of the hunting season was very low and not discernibly different for migrators and non-migrators. Non-hunting mortality also was low for migrating bears. In 10 years, 13 non-migrating bears were shot illegally during 15 July–15 October, or as a result of nuisance activity, and one was hit by a car. No migrating bears were shot other than by legal hunters during that time and two were hit by cars on major highways.

Discussion

Most modern studies have not recognized bears as migrators, because their movements do not occur en masse and are not readily observed, but some historic accounts, drawing from traditional and anecdotal observations,

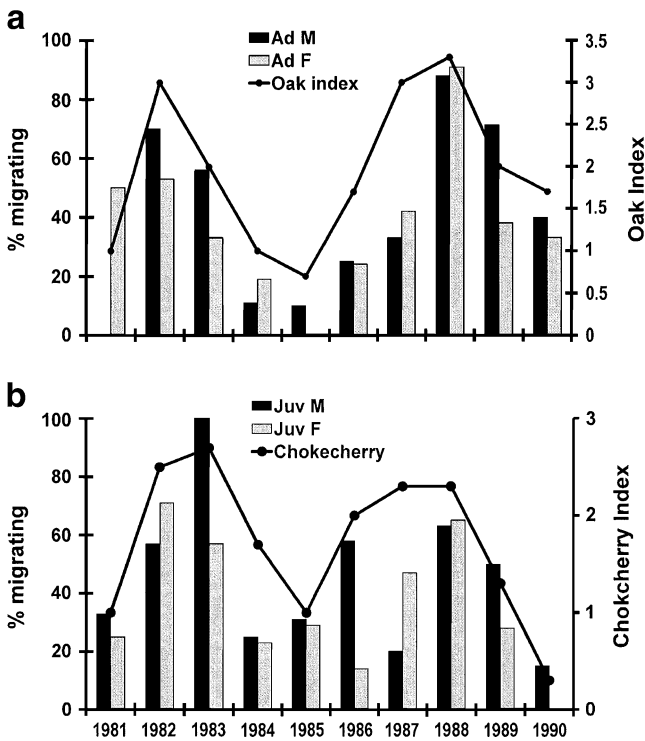


Fig. 3 Relationship between regional food abundance indices in north-central Minnesota and the proportion of **a** adult and **b** juvenile black bears, by sex, that made late-season migrations in north-central Minnesota, 1981–1990

recognized the migratory nature of these seasonal movements (Kudaktin and Chestin 1993; Schorger 1946). In areas with high topographic relief, black bears may not travel seasonally outside their summer range (Amstrup and Beecham 1976). In places where they do, they generally do not move as far as the bears in Minnesota (Garshelis and Pelton 1980, 2–18 km; Hellgren and Vaughan 1990, ≈5 km; Beck 1991, 8–23 km). The flat Minnesota landscape offers

less diversity in microclimate and habitat over short distances than more mountainous terrain, prompting longer travels to find key resources. These extensive late-season movements clearly fit within current paradigms for migration in being “straightened-out” travels that took place on a consistent temporal schedule and shifted animals among habitat zones (Dingle 1996). Migration was “partial,” in that not all animals participated, and “facultative,” in that it did not occur every year (Dingle and Drake 2007). In contrast, early-season forays were not coordinated in timing, direction, or destination, and may have been exploratory in nature, possibly aimed at assessing or enhancing breeding opportunities or as a precursor to dispersal (Klenner 1987; Lee and Vaughan 2003; Schwartz and Franzmann 1992). We focus discussion hereafter on our three hypotheses regarding variability in late summer migration patterns among individuals and year to year.

Hypothesis 1: Individuals leave their summer range in late summer if the likelihood is high that they will find better resources elsewhere Migration has generally been viewed as an adaptive response to adversity (Dingle 1996). This characterization fits the fall migration of temperate-nesting songbirds that flee northern latitudes as winter approaches and migrations of ungulates to wintering areas. Migrations, however, also include the movements of animals to areas with plentiful resources, such as the return of insects, birds and whales to northern latitudes in the spring. Likewise, some bear migrations have occurred in response to local food shortages: prime examples include the exodus of bears from Big Bend National Park during a year of extreme drought (Hellgren et al. 2005) and several similar cases elsewhere during extreme food failures (Pelton 1989; Schorger 1946). However, the salient feature of most bear migrations seems to be their orientation toward concen-

Table 4 Departure dates, duration of travel, and distance traveled for late-season bear migrations in north-central Minnesota during years with disparate food conditions, 1981–1990

Parameter	Sex/age	Year		
		1983 ^a	1988 ^b	Other years
Last date home (mean)	F 1–2 years	11 Sep	2 Aug	21 Aug
	F 3+years	20 Aug	3 Aug	16 Aug
	M 1–2 years	6 Aug	28 Jul	10 Aug
	M 3+years	25 Aug	3 Aug	13 Aug
Duration in days (mean)	F 1–2 years	19	57	31
	F 3+years	27	51	36
	M 1–2 years	20	63	46
	M 3+years	28	50	41
Distance in km (median)	F 1–2 years	8	24	5
	F 3+years	7	20	8
	M 1–2 years	27	33	23
	M 3+years	8	22	18

^a Highest chokecherry abundance during the study

^b Highest oak abundance during the study, particularly bur oak

Fig. 4 Contrasting migration patterns of female black bears inhabiting the Chippewa Plains lowlands (a, c) and those in the adjacent Suomi Hills uplands (b, d) in north-central Minnesota. Each *solid symbol* denotes a different bear on its summer home range. *Open symbols* depict destinations of each migration event, so bears that migrated multiple years show multiple destinations. Typically (1981–1990, excluding 1988) about 50% of lowland females migrated, usually to the nearby Suomi Hills (a), whereas Suomi Hills residents rarely moved (b). However, in 1988, nearly all females left their home ranges and bypassed the Suomi Hills to travel southwest of the study area to stands of bur oak and agricultural fields (c, d)

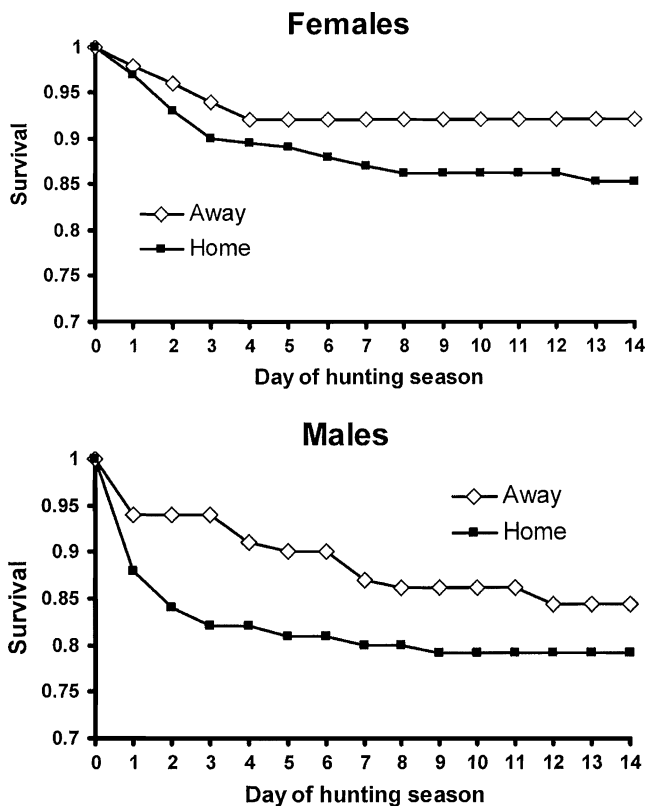
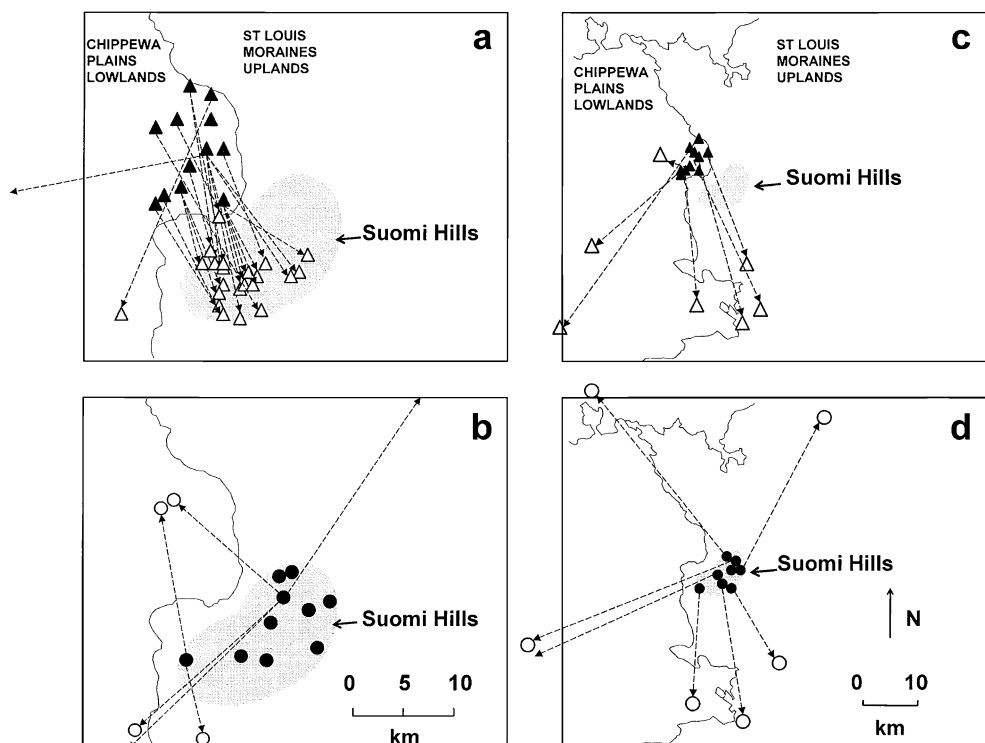


Fig. 5 Cumulative survival of radio-collared black bears that remained on their summer home range during the first 2 weeks of Minnesota's bear hunting season (1–14 September) vs survival of bears on seasonal migrations, 1981–1990

trations of preferred foods (Garshelis and Pelton 1981; Hellgren and Vaughan 1990; Schwartz and Franzmann 1991). Bears in this study migrated primarily south and southwest, along an increasing food gradient (Noyce, unpublished data). Statewide food surveys indicated that oak trees, particularly bur and white oak (*Quercus alba*), were more abundant in the hardwood forests that were common south of our study area. Bears and many species prefer these acorns to those of red oak, presumably due to their lower tannin content (Kirkpatrick and Pekins 2002).

As large animals that feed on scattered, small food items, bears must employ an “energy-maximizing” strategy (Welch et al. 1997), focusing on food patches that provide the highest return of calories. Moreover, fruits and nuts, which are favored bear foods, are masting species, meaning that they produce small-to-moderate crops most years, but occasionally a massive over-abundance that is often synchronized over large distances (Koenig and Knops 2000). Despite general synchrony, dispersion and local density of these plants are highly variable. Mast abundance within an animal's home range may thus be a signal that hot spots may exist elsewhere, whereas mast failure at home suggests there may be little to gain by leaving.

The chance of finding better foods elsewhere is also a function of mobility and the types and quality of habitat that an animal is likely to encounter (Sabine et al. 2002). In our study, lowland female bears frequently moved south to the nearby Suomi Hills to seek red oak acorns. The risks entailed in this short move were minimal, for even if acorns

were scarce, the upland forest habitat was still likely to provide better fall food than their lowland home ranges (Noyce and Coy 1990). In years of food failure, however, even these bears, apparently cueing on local scarcity, chose not to move and instead subsisted on less preferred foods, such as vegetation and insects (Garshelis and Noyce 2008). Suomi Hills females, who lived in the best local habitat, had less to gain from migrating, and finding better foods would likely require traveling much longer distances. However, in 1988, an exceptional crop of bur oak acorns, which were uncommon locally but more available south and west of the study area, was sufficient to entice these bears and others from across the study area to forego a reasonable local crop of red oak acorns and travel unusually long distances to take advantage of the bounty.

Migrators that move in response to food scarcity are often highly mobile specialists that must leave their home area when key foods fail (Newton 2006; Fox et al 2009). Black bears can move long distances, but not enough to escape the winter dearth of foods. Their strategy is to eat as much as possible, and store sufficient energy in the form of fat to sustain them through an extended hibernation fast. To maximize weight gain, bears are drawn to food abundance and thus make long distance migrations when they have reason to believe that rich food sources exist on the landscape; they may also be forced to migrate in cases of extreme food scarcity, although that was never the case on our study site. How bears and other migrators make decisions about whether, where and when to migrate in search of foods that are beyond their normal range of familiarity and, at least initially, beyond their sensory detection, apparently relying on environmental and social cues, remains an intriguing question (Kenney et al 2001).

Hypothesis 2: Individuals are most likely to travel in search of better foods if their body mass is close to a reproductive or survival threshold Because migration is risky and potentially energetically costly, we presumed that animals with the most to gain (e.g., earlier attainment of sexual maturity) would also be most inclined to take such a risk. Previously, Noyce and Garshelis (1994) identified three significant body mass thresholds (measured in late winter) for female black bears: (1) those weighing <41 kg never produced cubs the following year; (2) below 65 kg, but not above, maternal body mass was positively related to fecundity and to growth and survival of cubs; (3) further positive effects of body mass on reproduction were not apparent until bears reached about 90 kg. Average late-winter mass of female bears in the CNF was 35 kg at 2 years old and 46 kg at 3 years old (Noyce and Garshelis 1998). Few individuals reached 41 kg by age 2, but most could attain it by age 3, with ample foods as 2-year-olds. Our findings here that 2- and 3+-year-olds weighing 35–

50 kg were the most likely to migrate supports our hypothesis, as those bears were close to the 41-kg weight threshold. Moreover, particularly heavy yearlings could reach 41 kg in a year, whereas smaller bears could not, so the greater propensity of heavy yearlings to migrate also fits this hypothesis. In lowland habitats, body mass of first-time mothers averaged 58.4 kg (95% CI: 55.5–61.3) and multiparous females 68.7 kg (95% CI: 64.9–72.5), hence, close to the 65-kg threshold for increased litter size and survival. Upland females averaged 65.5 kg at first birth (95% CI: 62.6–68.5) and 90.6 kg (95% CI: 87.3–94.0) after that (Garshelis and Noyce 2008). Accordingly, lowland adult females migrated at twice the rate of upland females and upland adult females migrated only when unusual bur oak abundance put them within closer reach of the higher (90 kg) weight threshold. Males should be less tied to specific body mass thresholds. Instead, they should strive for ever-greater mass throughout their life, given that only a relative few of the largest males in an area have opportunity to sire cubs (Kovach and Powell 2003; Costello et al. 2009). This may explain the somewhat greater propensity for males in general to migrate.

Hypothesis 3: Travel behavior reflects decisions that minimize risk Risks faced by animals that migrate include failing to find sufficient food (to offset the cost of travel) and encountering increased threats of mortality due to the unfamiliar surroundings (Nicholson et al 1997). Our data suggest that bears acted cautiously in both their choice to migrate and their behavior during migration. Most minimized the risk of not finding adequate nutrition by staying home when regional food abundance was poor. As in other species (Sæther and Andersen 1990; Kohlmann and Risenhoover 1994), increased food abundance reduced this risk, encouraged greater movement, and perhaps enabled greater food selectivity. When chokecherry, a favored mid-summer food, was exceptionally plentiful, as in 1983, bears took advantage of this by delaying departure and shortening the duration of their late-season migrations (also noted by Garshelis and Pelton 1981). But it was primarily oaks, which can create some of the highest caloric densities on the landscape (Inman and Pelton 2002), that drew bears away from home. These trees seem to have a keystone effect on bears and other species across large areas of North America (Pelton 1989; Vaughan 2002).

Potential risks during migration are, for most species, greatest for juveniles. Juvenile bears are the most vulnerable to predation and cannibalism (Garshelis 1994; Samson and Huot 1998), undernutrition (Noyce and Garshelis 1994), and possibly spatial disorientation (Landriault et al. 2006). Accordingly, yearling females, the smallest bears, were the least likely to migrate. Those that did migrate traveled shorter distances than older bears and appeared to

cue their movements on different foods (especially cherries). Small-bodied bears can achieve maximal weight gains while feeding on small fruits, whereas adults require more calorie-dense foods, like nuts (Welch et al. 1997). Cherries were dispersed in small patches across habitat types and fruit sometimes persisted late into the summer, providing small bears with excellent forage without necessitating extensive travel or exposure to larger animals that may have congregated at richer feeding sites.

The low hunting mortality of bears that were outside their home ranges during the hunting season suggested a reticence to visit hunters' baits when bears were in unfamiliar settings. Similarly, Brown and Alkon (1990) found that porcupines (*Erethizon dorsatum*) adopted specific vigilance behaviors in particularly risky habitat conditions, and thereby greatly reduced mortality risk. Also, it has been observed that many species of migrating animals tend to move directly toward a destination and bypass food resources that normally would be of interest (Dingle 1996; Dingle and Drake 2007). Rogers (1989) found that radio-collared black bears traveling home from forays followed straight-line trajectories, often at night, forgoing trails and foraging. Studies that reported increased mortality for bears that left their summer range regarded dispersing males (Elowe and Dodge 1989; Schwartz and Franzmann 1992), whose behavior appears to be quite different than seasonal migrants.

From an evolutionary standpoint, animals would not migrate if it were not adaptive, but that is not to say that each individual, faced with the annual choice of whether to do so, chooses correctly. The inherent conundrum of measuring whether an individual is better off than it would have been had it behaved differently is self-evident. Comparisons of outcomes for conspecifics that did and did not migrate are compromised by the unique and complex suite of factors that influence each individual's behavior each year. Longitudinal tracking of individuals through multiple years presents similar problems, as age, reproductive status, and habitat conditions change yearly. In our study, opportunities for such comparisons were further limited by the rapid turnover of individuals due to hunting. In human-dominated landscapes, long-term evolutionary advantages of a behavior like migration could be overridden by threats introduced by humans. Our findings suggest that vigilance behaviors evolved in bears during travel may protect them from some manmade dangers (hunters, other bears at hunters' baits) but perhaps not all (cars). Factors including year-specific resource distribution and each bear's nutritional condition, physical stature, social dominance, age, experience, and personality, all likely inform its decision about whether to travel, and if so, when and where to go. Recent theoretical and empirical evidence support the idea that multiple behavioral strategies may be successful

within populations living where environmental conditions vary from year to year (Dingemanse and Réale 2005; Kaitala et al. 1993; Nicholson et al. 1997).

Crucial to successful seasonal migrations are high mobility and well-developed navigational ability, characteristics that are evident in bears (Landriault et al. 2006; Rogers 1987b; Sauer et al. 1969). A remarkable physiologic lability enables bears to derive maximum benefit from periodic nutritional bursts like masting, insect outbreaks, and fish spawns: even young bears whose growth has been severely curtailed in a year of food shortage can fully rebound with abundant resources the following year (Noyce and Garshelis unpublished data). We suggest that in bears, high intelligence, in tandem with migratory flexibility, complement these characteristics to create a population of individuals poised to take maximum advantage of a highly stochastic environment.

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